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Carboniferous and Permian Leaioidea (Branchiopoda: Conchostraca) from Australia: Taxonomic Revision and Biostratigraphic Implications

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ABSTRACT. A taxonomic revision of Australian leaioid faunas has reduced, by synonymy, the known Early Carboniferous taxa to three species viz., *Hemicycloleaia andersonae* (Tasch, 1979), *H. grantrangicus* (Tasch, 1979) and *Rostroleaia carboniferae* (Tasch, 1979); and the known Late Permian taxa to three species viz., *Hemicycloleaia mitchelli* (Etheridge, 1892), *H. discoidea* (Mitchell, 1925), and *H. deflectomarginis* (Tasch, 1979). The revision establishes a consistent taxonomic nomenclature to facilitate comparisons with extra-Australian leaiid species, and their correlations. Particular attention is paid to the correlation of the Late Permian leaioid and estheriid faunas of the Newcastle Coal Measures (NCM) of the Sydney Basin, with those of the Lebedevian of the Lower Tungus and Nordvik Basins, northern Siberia, which in turn, indicate a correlation (Lozovsky, 1998) with the Late Tatarian Vjatian (Luptug member) horizon of the Russian Platform. We speculate that the conchostracans may have lived in estuaries and ephemeral relict water bodies along a coastal plain, and that their eggs were dispersed either by wind, by minor marine incursions, or by both of these processes. Such marginal marine influences could partly explain the widespread distribution of Mitchell's Late Permian (Tatarian) conchostracan species.

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The Conchostraca are small branchiopod crustaceans with a weakly mineralised bilaterally compressed shell, in which the valves are joined by a ligament in a simple elevated fold. Post-Palaeozoic species appear to have lived in a lacustrine milieu, as do extant species; but some Palaeozoic species may have been adapted to brackish paralic environments (Webb, 1979; Chen & Shen, 1985). Like the Ostracoda, they are potentially useful biostratigraphic and palaeoecologic indicators. The Leaioidea are easily distinguished from other superfamilies of Conchostraca on the basis of valves bearing up to five radial carinae, which first appear in the ontogeny on the umbo, and in later growth stages extend towards the free margin. Leaioids first appear in the geological record, together with representatives of other superfamilies (Estheriteoidea, Eosestherioidea, and Lioestherioidea), in the Devonian. Unlike these taxa, which are well represented in the Mesozoic, with some families still extant, the leaioids appear to have become extinct by the end of the Palaeozoic.

Published research on Australian leaioid conchostracans has so far been concentrated on faunas from the Lower Carboniferous, and the Upper Permian. Early Carboniferous leaioid taxa were described from the subsurface Anderson Formation, in the Canning Basin, Western Australia (Tasch & Jones, 1979); and from the Raymond Formation in the Drummond Basin, Queensland (Tasch, 1979). Late Permian leaiids were described from the Newcastle Coal Measures (NCM) in the Sydney Basin (Etheridge, 1892; Mitchell, 1925); these were the first leaiids to be reported from Australia, at a time when very little was known about Palaeozoic conchostracans. This pioneering work has been a major source reference for later taxonomic studies of leaiids in other parts of the world, several of which have misinterpreted Mitchell's (1925) type material, as discussed below. Tasch (1987) addressed these problems in a revision of Mitchell's material, which itself resulted in further problems. Other Late Permian leaiid taxa conchostracans have been described from the Blackwater Group in the Bowen Basin, Queensland (Tasch, 1979).

The aim of the present paper is to prepare a consistent taxonomy of the leaioid taxa from Australia to provide a comparison with those from overseas, and to evaluate their age significance. Particular attention has been paid to the correlation of the leaioid and estheriid faunas of the Upper Permian NCM. All type and figured specimens referred to in this paper are deposited in the Commonwealth Palaeontological Collection (under the prefix CPC) of the Australian Geological Survey Organisation (AGSO), formerly Bureau of Mineral Resources (BMR), Canberra; in the Palaeontological Collection of the Australian Museum, Sydney (under the prefix F); and in the Palaeontological Collection of the Department of Earth Sciences, University of Queensland, Brisbane (under the prefix UQF).

Previous studies of Australian Leaioid Conchostracan faunas

Sydney Basin. Leaiids were first found in Australia by John Mitchell in 1890, in loose chert that was used for road building at Charlestown, near Newcastle, New South Wales. The specimens were described by Etheridge (1892) under the name *Leaia mitchelli*, thirty years after Jones (1862) described the genus *Leaia* from the late Mississippian of North America. Mitchell (1925) described an additional 13 species referred to this genus and two unnamed species which he regarded as indeterminate, from material that he later collected *in situ* from localities within the Upper Permian NCM near Belmont and at Merewether Beach (Fig. 1).

Five of Mitchell's leaiid species were selected by overseas authorities (Kobayashi, 1954, and Novozhilov, 1952, 1954, 1956, 1958) as type species for new genera based, not on a first-hand examination of his material, but solely on his photographic figures, many of which had been retouched with black and white ink (Table 1). An additional five "new species" based on Mitchell's (1925) material, were introduced by Novozhilov (1956) [*Australoleaia miklouchomaklayi, Brachiorrhynchia chertensis*, and *Cycloleaia cyclica*], and by Kobayashi (1954) [*Trileaia sulcata* and *T. etheridgei*].

Subsequently, both Tasch (1969, 1979), and Chen & Shen (1985) considered that most of these genera are synonyms of *Leaia* Jones, 1862 or *Hemicycloleaia* Raymond, 1946. Tasch (1987) restudied and published new photographs of Mitchell's type specimens. By synonymy, he reduced the number of species introduced by Mitchell and Kobayashi from 16 to 12; the three species introduced by Novozhilov (1956) were not discussed. Tasch (1987) proposed one new species, *Leaia (Leaia) oblongoidea*, based on an incomplete carapace amongst Mitchell's illustrated specimens, and collected additional material from the NCM, from which he described a further three leaiid species [*L. (Hemicycloleaia) immitchelli, L. (H.) kahibahensis* and *L. (H.) magnumelliptica*]. Excluding the three above-mentioned "new species" introduced by Novozhilov (1956), which we regard as invalid (see below), the total number of leaiid species described from the NCM, after Tasch's (1987) analysis, stands at sixteen.

Bowen Basin. Leaiids were first recognised in the Bowen Basin by Dickins (in Veevers *et al*., 1964: 85) from the Upper Permian Blackwater Group, on the eastern flank of the northern part of the basin. A single sample consisting of three specimens was collected by M.A. Randal in 1960 from a locality (CL 314/6), about 79.5 km northeast of Clermont (Clermont 1:250 000 sheet; Fig. 2). Tasch (1979) described this limited material as a new species *Leaia (Hemicycloleaia) deflectomarginis* and "*Leaia (Hemicycloleaia)* sp. undet. 1".

Canning Basin. Carboniferous conchostracans were first recognised in Western Australia by Öpik (in McWhae *et al*., 1958), who identified leaiids in core samples taken from the Anderson Formation, penetrated by WAPET Grant Range No. 1 Well. This well (18°00'48"S 124°00'22"E) was

Table 1. List of Mitchell's (1925) leaioid species selected as type species for invalid genera introduced by Novozhilov (1952, 1954) and Kobayashi (1954).

Leaia quadriradiata	= *Brachioleaia* Novozhilov, 1952; *Quadrileaia* Kobayashi, 1954
Leaia discoidea	= *Cycloleaia* Novozhilov, 1952; *Discoleaia* Kobayashi, 1954
Leaia collinsi	= *Australoleaia* Novozhilov, 1954
Leaia quadrata	= *Gonioleaia* Novozhilov, 1952
Leaia belmontensis	= *Trileaia* Kobayashi, 1954

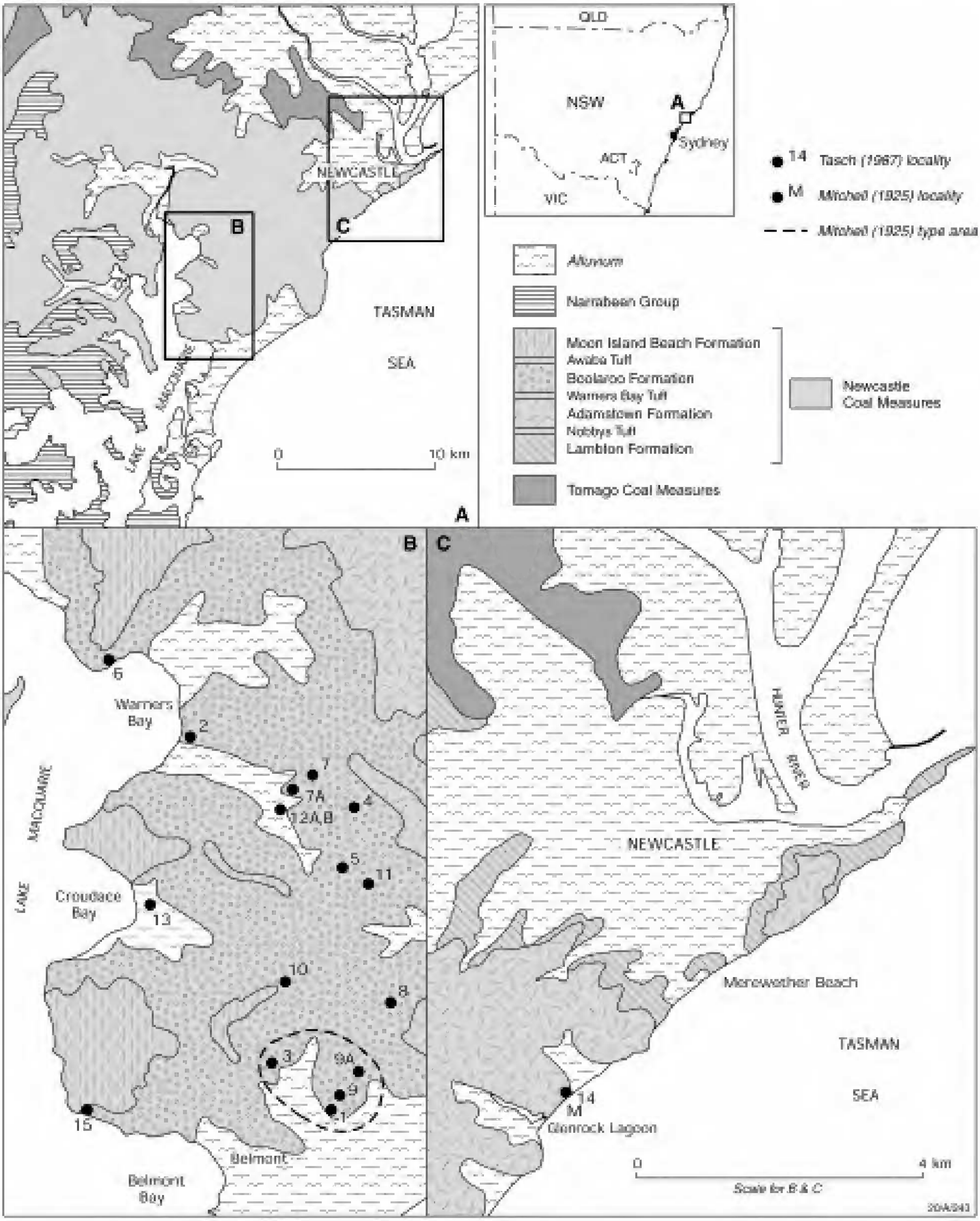

Figure 1. Locality maps Newcastle area, Sydney Basin. A—distribution of the Newcastle Coal Measures; B—distribution of conchostracan localities (Mitchell, 1925; Tasch, 1987) within the Boolaroo Formation in the Lake Macquarie area; C—distribution of conchostracan localities within the Lambton Formation (Mitchell, 1925, 1927; Tasch locality 14).

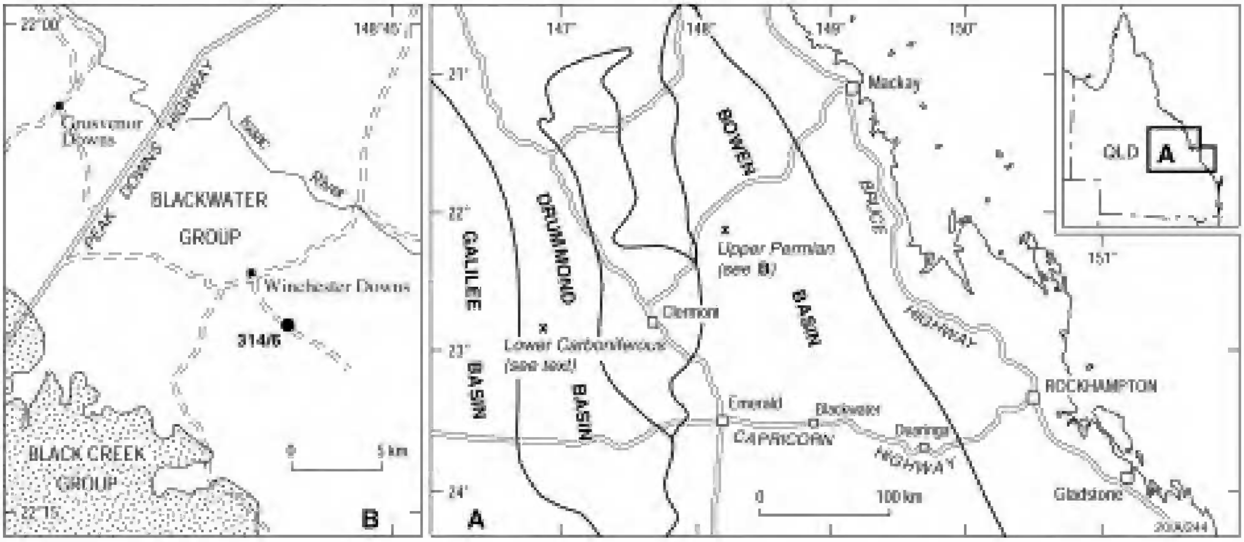

Figure 2. Locality maps of the Clermont area, Queensland, showing distribution of conchostracans in the Upper Permian Blackwater Group, Bowen Basin, and the Lower Carboniferous Raymond Formation, Drummond Basin.

drilled about 90 km south-southeast of Derby (Mount Anderson 1:250 000 sheet area) on the axis of the Grant Range Anticline within the Fitzroy Trough of the northern Canning Basin (Fig. 3). The sequence between 7900 feet (2408 m) and 12915 feet (3936 m; total depth) in Grant Range No. 1, designated by McWhae *et al.* (1958) as the type section of the Anderson Formation, consists of interbedded sandstone, siltstone and shale, with minor limestone, dolomite and anhydrite. Öpik determined the genus *Hemicycloleaia* in the leaiid sequence between 7907 and 8536 feet, which he regarded as Late Carboniferous (Westphalian-early Stephanian) in age. Bischoff (1968) concluded that this part of the sequence was deposited in a brackish estuarine or deltaic environment. The leaiid fauna was examined by Tasch (in Tasch & Jones, 1979), who described seven species belonging to four genera: *Monoleaia* Tasch, 1956, *Leaia* Jones, 1862, *Rostroleaia* Novozhilov, 1952, and *Limnadiopsileaia* Tasch, 1962. He also described two indeterminate species belonging to *Cyzicus*, and a species doubtfully referred to the Cretaceous genus *Ellipsograpta* Zhang, 1957.

Drummond Basin. Leaiid conchostracans were first recorded from Queensland by Hill (1957), who reported on collections made by Shell (Queensland) Development Pty Ltd geologists from two levels in the Lower Carboniferous sequence of the Drummond Basin (Olgers, 1972) viz., the top of the Telemon Formation, and the stratigraphically younger Ducabrook Formation. As a result of oil exploration by FRANCAREP, de Bretizel (1966) recorded a leaiid species from a third level, lying stratigraphically between these formations, from the Raymond Formation. This formation consists of quartzose sandstone and green mudstone, and attains a maximum thickness of 750 m in the southern part of the Drummond Basin (Playford & Jell, 1985). The leaiid specimens were collected by P. de Bretizel in 1963 from sites in the Narrien Range, 80 km W of Clermont (Galilee 1:250 000 sheet; Fig. 2). Although the precise localities are not known, they were collected from the top of section 70, and the base of section 75 (of de Bretizel, 1966: 83–84). The associated fauna included abundant fish (crossopterygian and palaeoniscoid) remains, malacostracan arthropods, and the polychaete annelid *Spirorbis* (Turner, 1993). In the absence of diagnostic marine fossils, this fauna is indicative of a brackish estuarine or deltaic environment (de Bretizel, 1966). For the same reason, a precise age for the Raymond Formation is difficult to determine; it may be within a ?late Tournaisian to early Viséan range. Turner (1993) suggested an early–mid Viséan age for the microvertebrate assemblage, which she described from the Raymond Formation. The leaiid species from the Raymond Formation, figured by Hill & Woods (1964) as *Leaia (Dolicholeaia?)* sp., was later described by Tasch (1979) as *Leaia (Hemicycloleaia) drummondensis*.

Localities and stratigraphic position of Late Permian conchostracan faunas

Bowen Basin. The leaioid species *Hemicycloleaia deflectomarginis* (Tasch, 1979) came from a single locality (CL 314/6) shown on the Clermont 1:250 000 sheet area (Olgers, 1969) at grid reference E 648767 N 2232877. M.A. Randal collected the specimens in 1960 from the Upper Permian Blackwater Group from a site 4.2 km SSE of Winchester Downs Homestead. This site is 2.0 km west of the westernmost limit of the CRA Limited Winchester South Coal Deposit (EPC486; Wilton, 1995). The stratigraphic position of the site is within the topmost Fort Cooper Coal Measures either within or just below the Yarrabee Tuff Bed; this tuff is overlain by the Rangal Coal Measures, the uppermost unit of the Blackwater Group (Fig. 9).

Sydney Basin. Mitchell's (1925) leaioid species came mainly from two areas within the NCM, the chert (tuff) quarries near Belmont (Fig. 1B), and the foreshore at Merewether Beach (Fig. 1C). Tasch's (1987) revision used

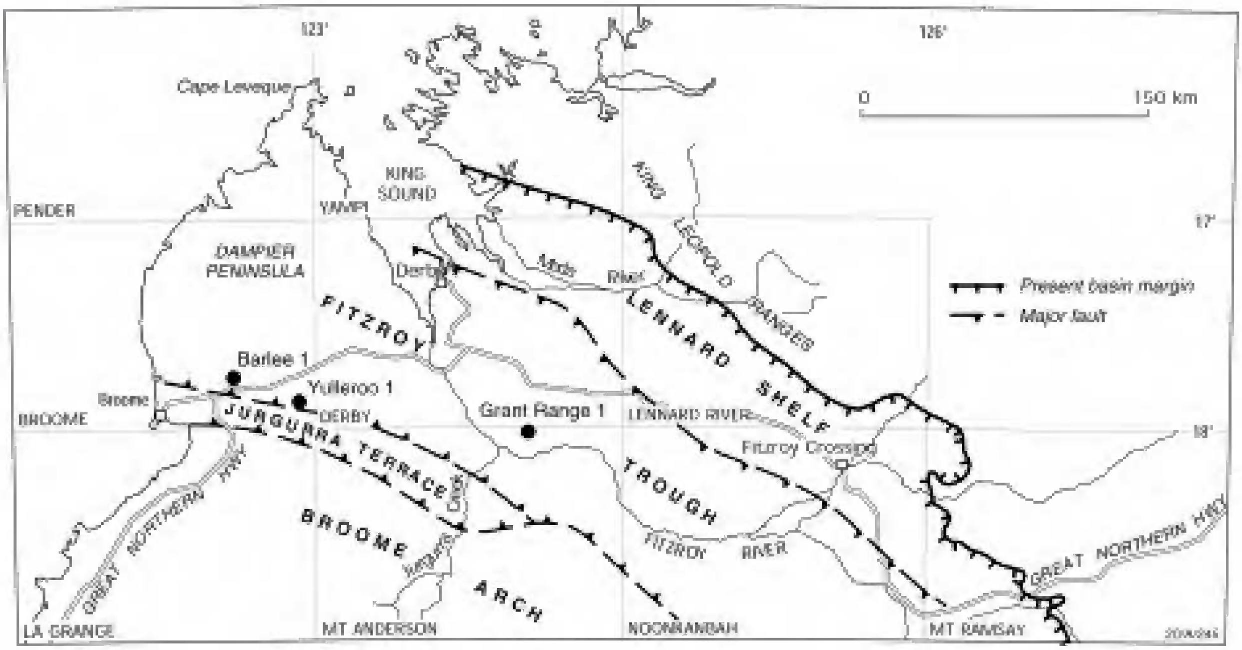

Figure 3. Locality map of the Fitzroy Trough, Canning Basin, showing the sites of those wells that contain Lower Carboniferous fossils within the subsurface Anderson Formation, which are discussed in the text.

the stratigraphic nomenclature and subdivision of the NCM after McKenzie & Britten (1969) and modified by the NSW Standing Committee on Coalfield Geology of NSW (1975). In this paper, the conchostracan localities of Mitchell (1925, 1927), and of Tasch (1987) are referred to the revised NCM stratigraphy as ratified by the NSW Standing Committee on Coalfield Geology in June 1992 (appendix 2 in Hawley & Brunton, 1995: 69–84), as modified by Little *et al.* (1996) (Fig. 4).

The Belmont localities contain two leaioid species (as revised here), *Hemicycloleaia discoidea* (Mitchell, 1925) and *H. mitchelli* (Etheridge, 1892), and three unribbed conchostracan species described by Mitchell (1927) as *Estheria belmontensis, E. glabra*, and *E. linguiformis*; [all three species referred by Raymond, 1946 to his genus *Pseudestheria*; and later referred by Tasch, 1987 to *Cyzicus (Euestheria); Palaeolimnadia (Palaeolimnadia)*; and *Palaeolimnadia? (Grandilimnadia?)* respectively]. The precise location of Mitchell's original Belmont site is equivocal. According to Knight (1970), Mitchell's original outcrop in the Belmont area was located 0.5 mile north of the John Darling Colliery, at a site 2.2 km NNE of Belmont. Its biota consists of leaioids associated with other conchostracans, and a *Glossopteris* flora came from a chert bed about 75 cm thick (the Belmont insect bed), that was later traced to other localities between Belmont and Warner's Bay on Lake Macquarie (Knight, 1970). Tasch, however, regarded a site on the northwestern shore of Belmont Bay (M15, Tasch, 1987, fig. 8), as Mitchell's original Belmont locality; this is based on a possible misinterpretation.

The only locality detail Mitchell provided for his Belmont leaioid and insect collections in the Newcastle Coal Measures was "chert quarries, near Belmont" (Mitchell, 1925: 441–443). He described the stratigraphic position of these localities as "a short distance above the old Cardiff Coal Seam [= Australasian Coal Seam (David, 1907: 251)] worked on the north-western shore of Belmont Bay (Great Northern Seam of David)" (Mitchell, 1925: 443). This statement matches the information Mitchell provided earlier to Tillyard (1917) on the stratigraphic position of the Belmont insect beds, but is in conflict with his correction, in the same paper (Mitchell, 1925: 439–440). The coal seam closest to, and above, the Belmont leaioid and insect fauna was misidentified by Mitchell as the Cardiff Seam. It is clear that this seam is the one bracketed by the Great Northern Coal above, and the Upper Pilot Coal below, which David (1907: 255) termed the Fassifern Seam.

Tasch (1987) correctly interpreted Mitchell's "old Cardiff Coal Seam" as the Fassifern Seam, and because Mitchell specified that the leaioids were above that coal seam, he inferred that Mitchell's original locality is within the Awaba Tuff. He then assumed that Mitchell's original site was on the northwestern shore of Belmont Bay (M15 in Tasch, 1987, fig. 8), but Tasch did not record conchostracans, or collect samples, from this site. However, we regard Mitchell's statement (quoted above) as simply implying a stratigraphic position, and not a precise geographic locality for the old Belmont chert (tuff) quarries. Mitchell's conchostracan specimens, which were associated with abundant insect remains, could have come from one or several of the localities visited and collected by Tasch (1987) e.g., his stations 3 (still named Belmont quarry), 1 (entrance to John Darling Colliery) and 9A,9B (just north of John Darling Colliery). Indeed, Knight (1970: 251) thought that Mitchell's original outcrop was located 0.5 mile north of the John Darling Colliery, at a site 2.2 km NNE of Belmont. Its biota, consisting of leaioids associated with other conchostracans and a *Glossopteris* flora, came from a chert (tuff) bed about 75 cm thick (the Belmont insect bed), that

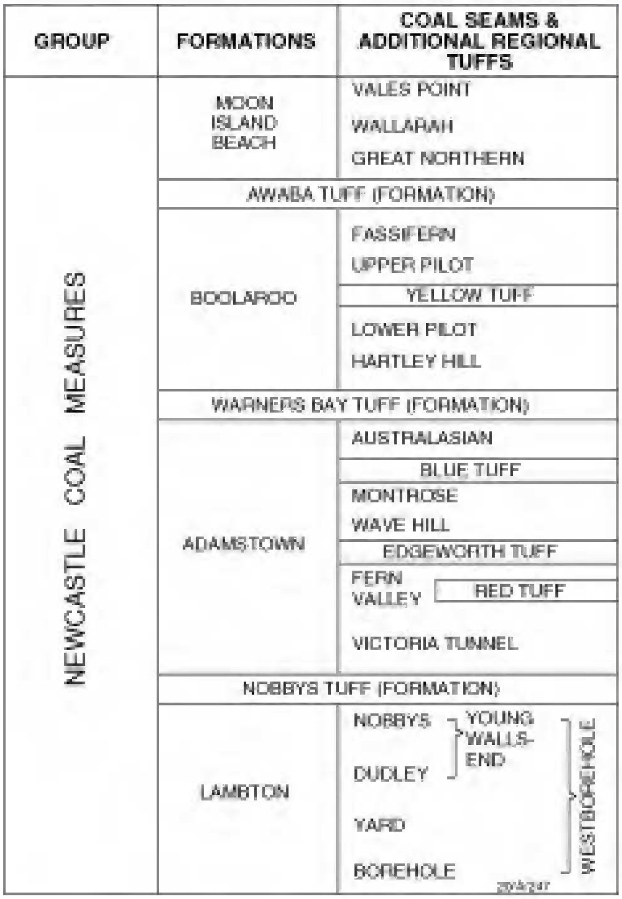

Figure 4. Current stratigraphic nomenclature of the Newcastle Coal Measures (after Hawley & Brunton, 1995, and Little *et al*., 1996, fig. 2).

was later traced to other localities between Belmont and Warner's Bay on Lake Macquarie (Knight, 1970). No ostracods have ever been found in association with the conchostracan samples.

According to Knight (1970) the Belmont insect bed is below the Fassifern Coal Seam, which suggests the same stratigraphic position for the leaioids in the Belmont chert (tuff) quarries. From Tasch's (1987: 19) study, the conchostracans in the Belmont area are distributed between the Upper Pilot Seam and the Fassifern Seam. Of all the localities from which he collected in the Belmont area, only two (Tasch stations 6 and 10) were above the Fassifern Seam. In terms of the revised NCM stratigraphy (appendix 2 in Hawley & Brunton, 1995), all the Belmont conchostracan localities of Mitchell (1925, 1927) and of Tasch (1987) were collected from the upper part of the Boolaroo Formation (Fig. 9).

The Merewether Beach locality (0.8 km NNE of Glenrock Lagoon; Fig. 1C) contains *Hemicycloleaia discoidea* (Mitchell, 1925), originally described as *Leaia compta*, from the Dirty Coal Seam (Mitchell, 1925: 445), which is now known as the Dudley Coal Seam. The label on the rock fragment containing the type specimen (F 25424) inscribed "From just above Dirty Seam", confirms Tasch's (1987: 23) comment that this species occurred above the Dudley seam. We presume this locality is the same one (i.e., "a short distance SW of the outflow of the Newcastle sewage") from which Mitchell (1927) described five unribbed conchostracans: *Estheria lenticularis* (type species of *Cyclestherioides* Raymond, 1946), *Estheria novocastrensis, E. lata, E. trigonellaris*, and *E. obliqua* [referred by Raymond, 1946 to his genus *Pseudestheria*; and by Tasch, 1987 to *Cyzicus (Euestheria)*], from "a few feet below the Dirty Seam ...". In terms of the revised NCM stratigraphy (appendix 2 in Hawley & Brunton, 1995), the Merewether Beach locality of Mitchell (1925, 1927) is in the upper part of the Lambton Formation. Tasch (1987: 259) subsequently collected from this locality (his station 14), a leaiid specimen (subsequently lost), *Cyzicus (Euestheria) novocastrensis*, and *C. (Euestheria) lata*.

Taxonomic revision of Australian Leaioidea

The taxonomy of fossil conchostracans is mainly based on the characteristics of the thin carapace and minute ornamentation of growth bands, because the soft bodies and appendages are seldom preserved in fossils (Chen & Hudson, 1991). For the superfamily Lioestherioidea, the morphological taxonomy is mostly dependent upon the features of the umbo (its size, whether it bears a node or spine) or dorsal margin (recurved growth lines near the dorsal margin); for the Eosestherioidea, it is based entirely on the variety of minute ornamentation of growth bands; and for the Leaioidea, the taxonomy is based on the numbers of radial carinae present, and partly on the recurved growth lines near the dorsal margin. In most fossil conchostracans, carapace outline varies only from elliptical, oval, or subquadrate to subcircular or semicircular, with umbones generally placed between the middle point and the anterior end of the dorsal margin; therefore differences in carapace outline are not regarded as superfamilial characters, but rather as characters (together with the number of growth lines) which serve to distinguish between species.

Within the Leaioidea, differences in angular measurements between radial carinae (Fig. 5) have been used by some authors (e.g., Tasch, Novozhilov) to distinguish taxa at the species level, but in our opinion, these may be due to variation within a single species. Furthermore, fossil conchostracans are susceptible to deformation and are often found in a crumpled state, and the deformational variation of *Hemicycloleaia tricarinata*, as described by Feys (1953) is particularly salutary in this regard. Thus, discrimination of species and genera on form alone becomes difficult and tends to result in long lists of subfamilies, genera and species based on forms which may well be conspecific.

Early Carboniferous Leaioidea. Our revision of the taxonomy of Early Carboniferous leaiids from the subsurface Anderson Formation (late Viséan-earliest Namurian?) is based on a re-examination of Tasch's type specimens (Tasch & Jones, 1979), and has reduced by synonymy the original 9 species (referred to 5 genera) to 3 species (referred to 2 genera), viz., *Hemicycloleaia andersonae* (Tasch, 1979), *H. grantrangicus* (Tasch, 1979)

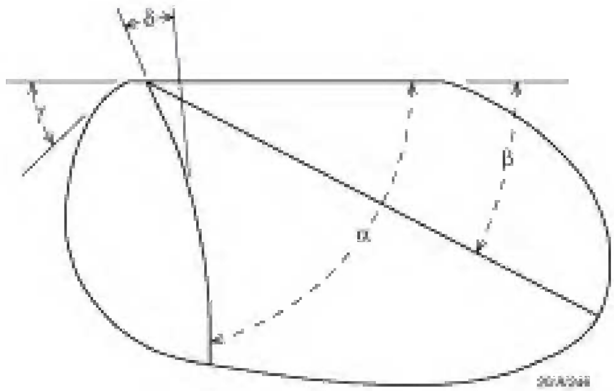

Figure 5. Leaioid conchostracan valve angles (after Tasch, in Tasch & Jones, 1979). Delta and gamma measure angular deviations from a straight line, represented respectively by the anterior rib (δ angle) and dorsal margin (γ angle). α and β angles are both measured from dorsal margin to the anterior rib (α angle) and posterior rib (β angle).

and *Rostroleaia carboniferae* (Tasch, 1979). Tasch & Jones (1979: 7) commented that the occurrence of *Monoleaia, Rostroleaia* and *Limnadiopsileaia* in the Anderson Formation represented the first records of these genera in pre-Permian rocks. Since then, Shen (1978, 1979) documented *Rostroleaia* in the Middle Devonian of South China, and in this paper we demonstrate that the specimens described as *Monoleaia australiata* Tasch, 1979 and *Limnadiopsileaia carboniferae* Tasch, 1979 belong to *Rostroleaia carboniferae* (Tasch, 1979). Also, we see no morphological reason to distinguish the Drummond Basin species, previously described as *Leaia (Hemicycloleaia) drummondensis* Tasch, from *Hemicycloleaia grantrangicus* from the Canning Basin (Table 2).

Late Permian Leaioidea. Our revision of the Late Permian leaiids from the NCM is based on a re-examination of Mitchell's (1925) type specimens, and a re-evaluation of Tasch's (1987) analysis of the same material. From our results, we consider that the taxonomies of Mitchell (1925) and other workers who have used his material (Kobayashi, 1954; Novozhilov, 1952, 1954, 1956, 1958; Tasch, 1987) represent examples of a tendency towards excessive splitting of fossil species (Table 3). An extreme example of this tendency, not only regards every specimen as a "new species", but also creates synonyms from Mitchell's syntypes, as exemplified by *Australoleaia miklouchomaklayi* Novozhilov, 1956 and *Cycloleaia cyclica* Novozhilov, 1956, which are objective junior synonyms of Mitchell's species *Leaia oblonga* and *L. discoidea*, respectively.

In our view, the number of species described by Mitchell (16, referred to the genus *Leaia*) should be reduced by synonymy to two, viz., *Hemicycloleaia mitchelli* (Etheridge, 1892) and *H. discoidea* (Mitchell, 1925). Furthermore, the four species described by Tasch (1987) from the NCM are junior synonyms of *H. mitchelli* (Etheridge, 1892). The limited material previously described from the Late Permian of the Bowen Basin as *Leaia (Hemicycloleaia) deflectomarginis* and *Leaia (Hemicycloleaia)* sp. indet. 1 (Tasch, 1979), belongs to a single species, *Hemicycloleaia deflectomarginis* (Tasch, 1979). Tasch (1979 p. 40, pl. 6, fig. 1) noted that the "slight downward flexure of the dorsal margin" in the latter species, is present in *Leaia pincombei* Mitchell, 1925 (a junior synonym of *Hemicycloleaia mitchelli* Etheridge, 1892; this paper). This feature, in both species, is probably due to crumpled preservation at the post-mortem stage.

Thus, three species of Late Permian leaioids are recognised in Australia viz., *Hemicycloleaia discoidea* (Mitchell, 1925), *H. mitchelli* (Etheridge, 1892) in the Sydney Basin, and *H. deflectomarginis* (Tasch, 1979) in the Bowen Basin. These species are larger, and have fewer growth bands, compared with those described from the Australian Carboniferous.

Table 2. Australian Leaiidae: Canning, Drummond and Bowen Basins.

Tasch, 1979 (in Tasch & Jones, 1979)	register number	revised name herein
Leaia (Leaia) andersonae	(CPC 17135)	= *Hemicycloleaia andersonae*
Leaia (Hemicycloleaia) rectangellipta	(CPC 17136)	= *Hemicycloleaia andersonae*
Monoleaia australiata	(CPC 17140)	= *Hemicycloleaia andersonae*
Leaia (Hemicycloleaia) grantrangicus	(CPC 17137)	= *Hemicycloleaia grantrangicus*
Leaia (Hemicycloleaia) tonsa	(CPC 17138)	= *Hemicycloleaia grantrangicus*
Leaia (Hemicycloleaia) longicosta	(CPC 17139)	= *Hemicycloleaia grantrangicus*
Leaia (Hemicycloleaia) drummondensis	(UQF 44310)	= *Hemicycloleaia grantrangicus*
Leaia (Hemicycloleaia) deflectomarginis	(CPC 17173A,B)	= *Hemicycloleaia deflectomarginis*
Leaia (Hemicycloleaia) sp. indet. 1	(CPC 17174)	= *Hemicycloleaia deflectomarginis*
Rostroleaia sp. (specimen destroyed)		= *Rostroleaia carboniferae*
	(CPC 33823; new)	= *Rostroleaia carboniferae*
Limnadiopsileaia carboniferae	(CPC 17141)	= *Rostroleaia carboniferae*

Table 3. Australian Leaiidae: Sydney Basin; list of species (Mitchell, 1925; Kobayashi, 1954; Tasch, 1987) regarded as junior synonyms of *Hemicycloleaia mitchelli* and *H. discoidea*.

***Hemicycloleaia mitchelli* (Etheridge, 1892)**	
Leaia mitchelli Etheridge, 1892	
Leaia mitchelli	(F 25426, F 25430, F 25487)
Leaia belmontensis Mitchell	(F 25429)
Leaia collinsi Mitchell	(F 25421)
Leaia elliptica Mitchell	(F 25463)
Leaia intermediata Mitchell	(F 25459)
Leaia oblonga Mitchell	(F 25420, F 25423)
Leaia ovata Mitchell	(F 25456)
Leaia paraleidyi Mitchell	(F 25454)
Leaia pincombei Mitchell	(F 25449)
Leaia quadrata Mitchell	(F 25468)
Leaia sp. indet., Mitchell	(F 25461) [= *Trileaia sulcata* Kobayashi, 1954]
Leaia sp. indet., Mitchell	(F 25427) [= *Trileaia etheridgei* Kobayashi, 1954]
Leaia (L.) oblongoidea Tasch	
Leaia (H.) immitchelli Tasch	
Leaia (H.) kahibahensis Tasch	
Leaia (H.) magnumelliptica Tasch	
***Hemicycloleaia discoidea* (Mitchell, 1925)**	
Leaia discoidea Mitchell	(F 25419; lectotype designed by Kobayashi, 1954)
	(F 25422; lectotype selected by Novozhilov, 1956)
Leaia compta Mitchell	(F 25421, in catalogue; F 25424)
Leaia latissima Mitchell	(F 25466)
Leaia quadriradiata Mitchell	(F 25465)

Systematic palaeontology

Order **Conchostraca** Sars, 1867

Suborder **Leaiina** Kobayashi, 1972

Superfamily **Leaioidea** Raymond, 1946

[*nom. transl.* Novozhilov, 1958; *ex* Leaiidae Raymond, 1946]

Remarks. The classification of the suborder Leaiina (*sensu* Kobayashi, 1972, 1973) adopted here differs from that proposed by Chen & Shen (1985), in that it is confined to the superfamily Leaioidea. This suborder originally included both the superfamilies Leaioidea Raymond, 1946 and Estheriellioidea Kobayashi, 1954.

The latter superfamily must now be excluded from the Conchostraca, and even from the Crustacea, because *Estheriella* Weiss 1875, the type-genus for both the family Estheriellidae and superfamily Estheriellioidea, must be referred to the Bivalvia. Investigations (by Chen Pei-ji) of the type specimens of the type species of *Estheriella* Weiss, 1875 [*E. costata* (Giebel 1857)], and of *Pseudestheriella* Novozhilov, 1956 [*Estheriella nodocostata* (Giebel, 1857); Jones, 1891], originally collected from the Lower Triassic Lower Bunter Sandstone of Germany, and now housed in the Natural History Museum, London (I 2533, I 2534 respectively), have confirmed Giebel's (1857) opinion that they have bivalve molluscan affinities.

At a lower supra-generic level, the subfamily Amphikoilinae Novozhilov, 1953, which was included by Chen & Shen (1985) in the family Leaiidae, must be also excluded from the Conchostraca, because Pogorevich (1975) has demonstrated that its type genus, *Amphikoilum* Novozhilov, 1953, is also a bivalve.

In this paper, we adopt the following modification of the earlier classification of Chen & Shen (1985) for the superfamily Leaioidea:

Monoleiolophidae—with one radial carina; includes *Monoleiolophus* Raymond, 1946, *Massagetes* Novozhilov, 1954, and *Petschoria* Zaspelova, 1962. [U. Carb.–U. Perm.]

Leaiidae—with two radial carinae and possibly a dorsal carina; includes *Leaia* Jones, 1862, *Hemicycloleaia* Raymond, 1946 and *Acantholeaia* Almeida, 1950. [M. Dev.–U. Perm.]

Praeleaiidae—with three to five radial carinae; includes *Praeleaia (Praeleaia)* Lutkevich, 1929, *P. (Hepuleaia)* Shen, 1978, *Paraleaia* Raymond, 1946 and *Eutrileaia* Shen, 1983. [M. Dev.]

Rostroleaiidae—with posterodorsally recurved growth bands along dorsal margin, and one to five radial carinae; includes *Rostroleaia* Novozhilov, 1952, *Limnadiopsileaia* Tasch, 1962 and *Pteroleaia* Copeland, 1962. [M. Dev.–U. Perm.]

Family **Leaiidae** Raymond, 1946

Diagnosis. Leaioidea with two radial carinae; a third carina may be present along the dorsal margin.

Genus ***Leaia*** Jones, 1862

1862 *Leaia* Jones, p. 116, pl. 5, figs. 11, 12.

Type species. *Cypricardia leidyi* Lea, 1855: 341 (by original designation); Upper Mississippian, Mauch Chunk Series (Chesterian), Pottsville, Pennsylvania, USA.

Diagnosis. Leaiidae with rectangular outline, bearing two radial carinae.

Range. Carboniferous.

Distribution. Europe?, North Africa and North America.

Remarks. It is difficult to separate transitional forms of *Leaia* and *Hemicycloleaia*, on the basis of carapace outline. In this paper, we prefer to confine the genus *Leaia* to those species with a rectangular carapace bearing two radial carinae, and without a dorsal carina.

Genus ***Hemicycloleaia*** Raymond, 1946

1946 *Hemicycloleaia* Raymond
1952 *Brachioleaia* Novozhilov
1952 *Cycloleaia* Novozhilov
1952 *Gonioleaia* Novozhilov
1952 *Dolicholeaia* Novozhilov
1952 *Kaltanleaia* Novozhilov
1952 *Lioleaia* Novozhilov
1953 *Leaia (Hemicycloleaia)* Raymond, Dechaseaux
1954 *Australoleaia* Novozhilov
1954 *Mimoleaia* Novozhilov
1954 *Siberioleaia* Novozhilov
1954 *Discoleaia* Kobayashi
1954 *Quadrileaia* Kobayashi
1954 *Trileaia* Kobayashi
1954 *Eoleaia* Kobayashi
1956 *Brachiorrhynchia* Novozhilov
1956 *Igorvarentsovia* Novozhilov
1965 *Cornoleaia* Molin
1969 *Leaia* Jones, Tasch
1978 *Kasacholeaia* Shen
1979 *Leaia (Hemicycloleaia)* Raymond, Tasch
1987 *Leaia (Hemicycloleaia)* Raymond, Tasch

Type species. *Hemicycloleaia laevis* Raymond, 1946: 286 (by origination designation); Upper Pennsylvanian, Conemaugh Series (Missourian) shale above lower Mahoning Sandstone, Conemaugh, Pennsylvania, USA.

Diagnosis. Leaiidae with elliptical, semicircular, subquadrate or ovate carapace, bearing two radial carinae; a third carina may be present along the dorsal margin.

Range. Middle Devonian to Upper Permian.

Distribution. Europe, Asia, Africa, North and South America, Australia and Antarctica.

Hemicycloleaia andersonae (Tasch, 1979)

Fig. 6a–d

1979 *Leaia (Leaia) andersonae* Tasch, p. 11, pl.1, fig. 1.
1979 *Leaia (Hemicycloleaia) rectangellipta* Tasch, p. 12, pl. 1, figs. 2–4.
1979 *Monoleaia australiata* Tasch, p. 13, pl. 2, fig. 4.
1987 *Leaia (Leaia) andersonae*; Tasch, p. 79.
1987 *Leaia (Hemicycloleaia) rectangellipta*; Tasch, p. 79.
1987 *Monoleaia australiata* Tasch, p. 79.

Diagnosis. Carapace small, elongate-elliptical or subelliptical anteriorly and subrectangular posteriorly in outline, 3.2–7.4 mm long and 1.9–4.4 mm high. Anterior carina somewhat arcuate and the posterior carina straight, dorsal margin thickened into third carina. α angle = 81–90°, β angle = 22–27.5°.

Remarks. With the exception of *Rostroleaia*, the eight species of Early Carboniferous leaioid conchostracans described by Tasch (in Tasch & Jones, 1979) from the Canning Basin, and the one species from the Drummond Basin, possess valves with two radial carinae, and a third carina, which is formed by a thickening of the dorsal margin. All species with these features may be referred to *Hemicycloleaia*. They can be subdivided into two groups based on the outline of the carapace: *H. andersonae* (Tasch) to include elliptical to subrectangular forms, and *H. grantrangicus* Tasch to include ovate to subsemicircular forms. An incomplete right valve described and figured by Tasch (in Tasch & Jones, 1979, pl. 2, fig. 4) as *Monoleaia australiata* possesses an anterior carina (Fig. 6b), which was concealed by incorrect lighting during photography.

Type locality and horizon. Grant Range No. 1 Well, core 62, 8530–8536 feet; Lower Carboniferous Anderson Formation. Also in core 52, 7907–7912 feet; same locality.

Hemicycloleaia grantrangicus (Tasch, 1979)

Fig. 6e–i

1964 *Leaia (Dolicholeaia?)* sp. Hill & Woods, p. c28, pl. cxiv, fig. 9.
1979 *Leaia (Hemicycloleaia) grantrangicus* Tasch, p. 12, pl. 1, figs. 5,6.
1979 *Leaia (Hemicycloleaia) tonsa* Tasch, p. 13, pl. 1, figs. 7,8.
1979 *Leaia (Hemicycloleaia) longicosta* Tasch, p. 13, pl. 2, figs. 1,2.
1979 *Leaia (Hemicycloleaia) drummondensis* Tasch, p. 39, fig. 5.
1987 *Leaia (Hemicycloleaia) grantrangicus*; Tasch, p. 79.
1987 *Leaia (Hemicycloleaia) tonsa*; Tasch, p. 79.
1987 *Leaia (Hemicycloleaia) longicosta*; Tasch, p. 79.
1987 *Leaia (Hemicycloleaia) drummondensis* Tasch, p. 79.

Diagnosis. Carapace broadly ovate or subsemicircular in outline, 4.3–7.8 mm long and 2.9–4.8 mm high. Short anterior carina gently arcuate and does not reach ventral margin; posterior carina generally long and bears weakly expressed nodes where growth lines cross it. α angle = 83–112.5°, β angle = 29–40°. Dorsal margin bears a carina reflected as a narrow flange.

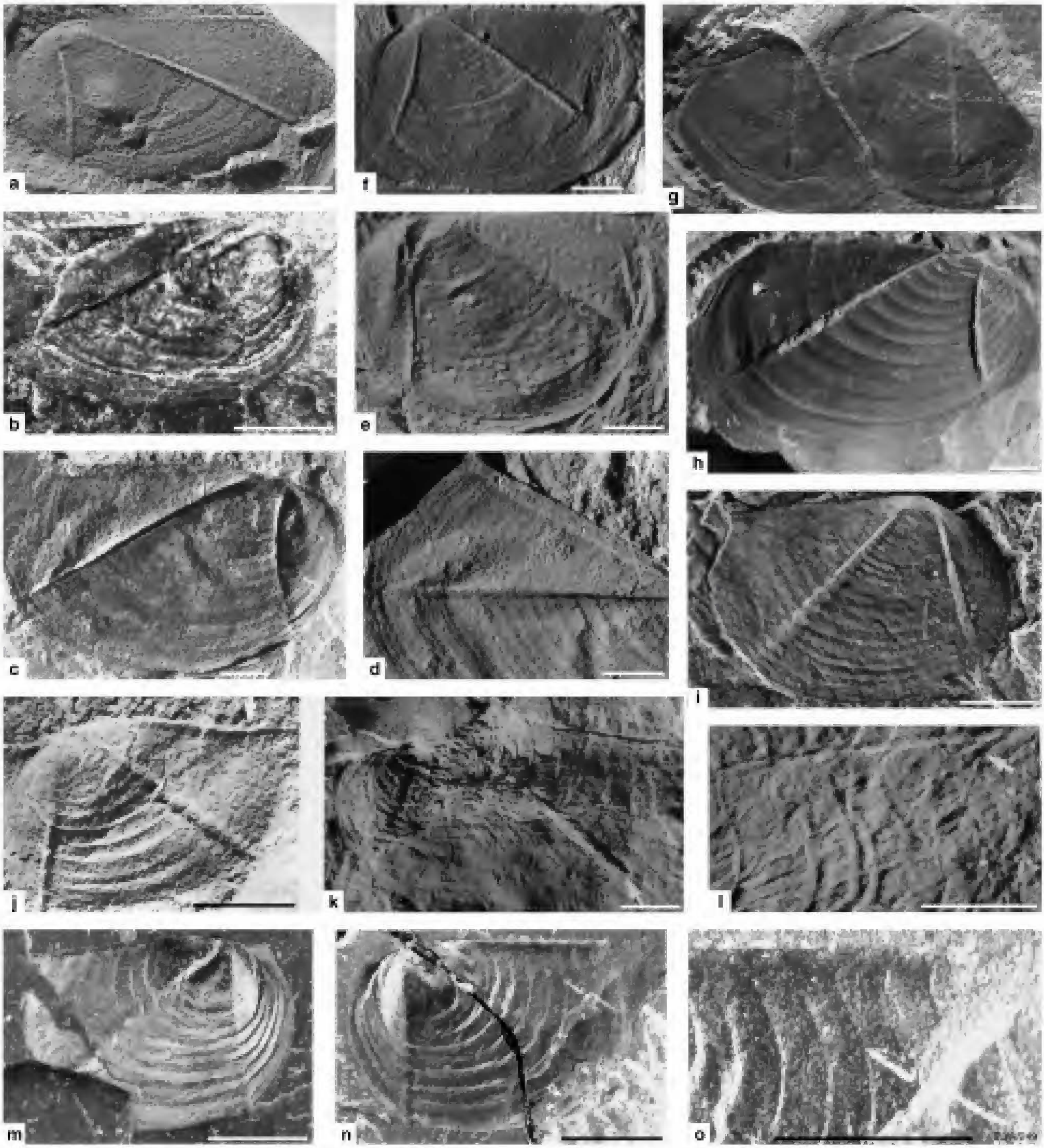

Figure 6. CARBONIFEROUS LEAIIDS, scale 1 mm. **a–d** *Hemicycloleaia andersonae* (Tasch): a—holotype, CPC 17135, left valve, WAPET Grant Range No. 1 Well, core 62 (8530–8536 feet), Anderson Formation; b—CPC 17140 (formerly *Monoleaia australiata* Tasch), right valve, WAPET Grant Range No. 1 Well, core 52 (7907–7912 feet), Anderson Formation; c,d—CPC 17136 (formerly *Leaia (H.) rectangellipta* Tasch), external mould of left valve, same locality as for b. **e–i** *Hemicycloleaia grantrangicus* (Tasch): e—CPC 17139 (formerly *Leaia (H.) longicosta* Tasch), external mould of right valve, same locality as for b; f,g—CPC 17138 (formerly *Leaia (H.) tonsa* Tasch), f, left valve, g, same left valve on right side and an internal mould of right valve on left side, WAPET Grant Range No. 1 Well, core 62 (8530–8536 feet), Anderson Formation; h—holotype, CPC 17137, right valve, WAPET Grant Range No. 1 Well, core 52 (7907–7912 feet), Anderson Formation; i—UQF 44310 (formerly *Leaia (H.) drummondensis* Tasch), right valve, Narrien Range, NW of Emerald, Drummond Basin, Raymond Formation. **j–o** *Rostroleaia carboniferae* (Tasch): j—specimen destroyed, (formerly *Rostroleaia* sp. Tasch), left valve, same locality as for h; k,l—holotype, CPC 17141 (formerly *Limnadiopsileaia carboniferae* Tasch), k, broken left valve (arrow points to the posterior radial carina) and partly external mould of another right valve with anterior radial carina, l, arrow points to the recurved posterodorsal margin, same locality as for h; m–o—CPC 33823 (new selected specimen from the original collection), m, external mould of left valve, same locality as for h, n, left valve, o, same specimen showing the recurved growth bands near the posterodorsal margin.

Remarks. We include *Leaia (Hemicycloleaia) tonsa* Tasch and *L. (H.) drummondensis* Tasch, as junior synonyms of *Hemicycloleaia grantrangicus*. Although the holotypes of *H. tonsa* and *H. drummondensis* possess more growth lines and have a slightly greater height/length ratio (0.67, 0.73), compared to the holotype of *H. grantrangicus* (0.62), we attribute these differences to ecophenotypic variation within a single species. As revised here, *Hemicycloleaia grantrangicus* differs from *H. andersonae* only in the configuration of the carapace. It has a height/length ratio ranging between 0.62 and 0.73, whereas in *H. andersonae* this ratio is less than 0.59. This difference could be due to dimorphism, because within other samples of leaiid populations, the valve of the female is frequently shorter than the otherwise similar male, which in turn, is generally narrower than the female. Thus *H. grantrangicus* and *H. andersonae* may be dimorphs of a single species.

Type locality and horizon. Grant Range No. 1 Well, cores 52, 7907–7912 feet; Lower Carboniferous Anderson Formation, Canning Basin, Western Australia. Also in core 62, 8530–8536 feet, same locality; and in Narrien Range, NW of Emerald, Lower Carboniferous Raymond Formation, Drummond Basin, Queensland.

Hemicycloleaia mitchelli (Etheridge, 1892)

Fig. 7a–n

1892 *Leaia mitchelli* Etheridge, p. 307.
1925 *Leaia mitchelli*; Mitchell, p. 440, pl. 41, figs. 1,2.
1925 *Leaia belmontensis* Mitchell, p. 445, pl. 42, fig. 15.
1925 *Leaia collinsi* Mitchell, p. 446, pl. 43, fig. 16.
1925 *Leaia elliptica* Mitchell, p. 443, pl. 42, fig. 10.
1925 *Leaia intermediata* Mitchell, p. 440–441, pl. 41, figs. 3–4.
1925 *Leaia oblonga* Mitchell, p. 441, pl. 41, fig. 5, pl. 43, fig. 18.
1925 *Leaia ovata* Mitchell, p. 443–444, pl. 42, fig. 12.
1925 *Leaia paraleidyi* Mitchell, p. 442–443, pl. 41, fig. 8.
1925 *Leaia pincombei* Mitchell, p. 443, pl. 42, fig. 9.
1925 *Leaia quadrata* Mitchell, p. 446, pl. 43, fig. 17.
1925 *Leaia* sp. indet., Mitchell, p. 446, pl. 43, fig. 20.
1925 *Leaia* sp. indet., Mitchell, p. 446, pl. 43, fig. 21.
1952 *Gonioleaia quadrata* (Mitchell); Novozhilov, p. 1371, fig. 2d (= drawing of Mitchell, 1925, pl. 43, fig. 17).
1954 *Trileaia mitchelli* (Etheridge) Kobayashi, p. 108, 144–145, 161.
1954 *Trileaia belmontensis* (Mitchell); Kobayashi, p. 144, text-fig. 30 l.
1954 *Trileaia etheridgei* Kobayashi; Kobayashi, p. 108, 144, 157.
1954 *Trileaia intermedia* [sic] (Mitchell) Kobayashi, p. 108, 145, 158.
1954 *Trileaia sulcata* Kobayashi; Kobayashi, p. 108, 144, 145.
1954 *Leaia collinsi* Mitchell; Kobayashi, p. 155.
1954 *Leaia elliptica* Mitchell; Kobayashi, p. 108, 166.
1954 *Leaia oblongata* [sic] Mitchell; Kobayashi, p. 109, 163.
1954 *Leaia ovata* Mitchell; Kobayashi, p. 163.
1954 *Leaia paraleidyi* Mitchell; Kobayashi, p. 163.
1954 *Leaia pincombei* Mitchell; Kobayashi, p. 164.
1954 *Australoleaia collinsi* (Mitchell); Novozhilov, p. 1241–1244.
1956 *Mimoleaia mitchelli* (Etheridge); Novozhilov, p. 63, pl. 11, fig. 3 (= Mitchell, 1925, pl. 41, fig. 2).
1956 *Australoleaia collinsi* (Mitchell); Novozhilov, p. 71, pl. 12, fig. 4 (= Mitchell, 1925, pl. 43, fig. 16).
1956 *Australoleaia miklouchomaklayi* Novozhilov; Novozhilov, p. 70, 71, pl. 12, fig. 3 (= *Leaia oblonga* Mitchell, 1925, pl. 43, fig. 18 only).
1956 *Hemicycloleaia belmontensis* (Mitchell); Novozhilov, p. 38, pl. 6, fig. 8 (= Mitchell, 1925, pl. 42, fig. 15).
1956 *Hemicycloleaia etheridgei* (Kobayashi); Novozhilov, p. 39, pl. 6, fig. 9 (= Mitchell, 1925, pl. 43, fig. 21).
1956 *Hemicycloleaia intermediata* (Mitchell); Novozhilov, p. 32, pl. 4, figs. 9,10. (Included *L. intermediata* pl. 41, fig. 3 and *L. elliptica* pl. 42, fig. 10).
1956 *Hemicycloleaia pincombei* (Mitchell); Novozhilov, p. 32, pl. 4, fig. 8 (= Mitchell, 1925, pl. 42, fig. 9).
1956 *Hemicycloleaia sulcata* (Kobayashi); Novozhilov, p. 39, pl. 6, fig. 10 (= Mitchell, 1925, pl. 43, fig. 20).
1956 *Leaianella paraleidyi* (Mitchell); Novozhilov, p. 58, pl. 10, fig. 2 (= Mitchell, 1925, pl. 41, fig. 8).
1956 *Mimoleaia ovata* (Mitchell); Novozhilov, p. 65, 66, pl. 11, fig. 8 (= Mitchell, 1925, pl. 42, fig. 12).
1956 *Siberioleaia oblonga* (Mitchell); Novozhilov, p. 26, 27, fig. 18, pl. 3, fig. 6 (= Mitchell, 1925, pl. 41, fig. 5 only).
1956 *Gonioleaia quadrata* (Mitchell); Novozhilov, p. 83, pl. 14, fig. 5 (= Mitchell, 1925, pl. 43, fig. 17).
1965 *Mimoleaia mitchelli*; (Etheridge); Novozhilov, pl. 6, figs. 1–3.
1965 *Leaianella paraleidyi*; (Mitchell); Novozhilov, pl. 7, figs. 5,6.
1987 *Leaia (Hemicycloleaia) mitchelli* Etheridge; Tasch, p. 82, 120–122, pl. 23, fig. 1, pl. 40, fig. 1, 2, pl. 41, fig. 1,4.
1987 *Leaia (Hemicycloleaia) collinsi* Mitchell; Tasch, p. 79, 122, pl. 22, fig. 3, pl. 40, fig. 3.
1987 *Leaia (Hemicycloleaia)* cf.*collinsi* Mitchell; Tasch, p. 80.
1987 *Leaia (Hemicycloleaia) elliptica* Mitchell; Tasch, p. 80, 125, pl. 23, fig. 4, pl. 41, fig. 7.
1987 *Leaia (Hemicycloleaia) etheridgei* (Kobayashi); Tasch, p. 126, pl. 41, fig. 6.
1987 *Leaia (Hemicycloleaia)* cf. *etheridgei* (Kobayashi); Tasch, p. 80, pl. 22, fig. 6.
1987 *Leaia (Leaia) oblonga* Mitchell; Tasch, p. 82,83, 123, pl. 23, fig. 6, pl. 40, fig. 7.
1987 *Leaia (Hemicycloleaia) ovata* Mitchell; Tasch, p. 83, 126, 127, pl. 24, fig. 2, pl. 41, fig. 8.
1987 *Leaia (Hemicycloleaia) paraleidyi* Mitchell; Tasch, p. 124, pl. 42, fig. 8.
1987 *Leaia (Hemicycloleaia)* cf. *paraleidyi* Mitchell; Tasch, p. 83, pl. 24, fig. 4.
1987 *Leaia (Hemicycloleaia) pincombei* Mitchell; Tasch, p. 122, 123, pl. 40, fig. 4.
1987 *Leaia (Hemicycloleaia) sulcata* (Kobayashi); Tasch, p. 127, pl. 41, fig. 3.
1987 *Leaia (Hemicycloleaia) oblongoidea* Tasch, p. 83, 124, pl. 24, fig. 1, pl. 40, fig. 8.
1987 *Leaia (Hemicycloleaia) belmontensis* Mitchell; Tasch, p. 79, pl. 22, fig. 2.
1987 *Leaia (Hemicycloleaia) immitchelli* Tasch, p. 80, 81, pl. 23, fig. 2.
1987 *Leaia (Hemicycloleaia) kahibahensis* Tasch, p. 81, pl. 24, fig. 3.
1987 *Leaia (Hemicycloleaia) magnumelliptica* Tasch, p. 81, 82, pl. 22, fig. 5.

Diagnosis. Carapace moderate to large in size and subovate in outline. 4.2–8.0 mm in length, 3.0–5.8 mm in height. Anterior radial carina slightly arcuate, posterior radial carina long and straight, both reaching to or near the ventral margin of the valve. Dorsal margin thickened into a third carina. Sometimes a short embryonic carina (see arrow, Fig. 7a,h), which is not present on all specimens of this species, originates near the dorsal margin slightly beyond the main posterior carina and deviates slightly from the dorsal margin.

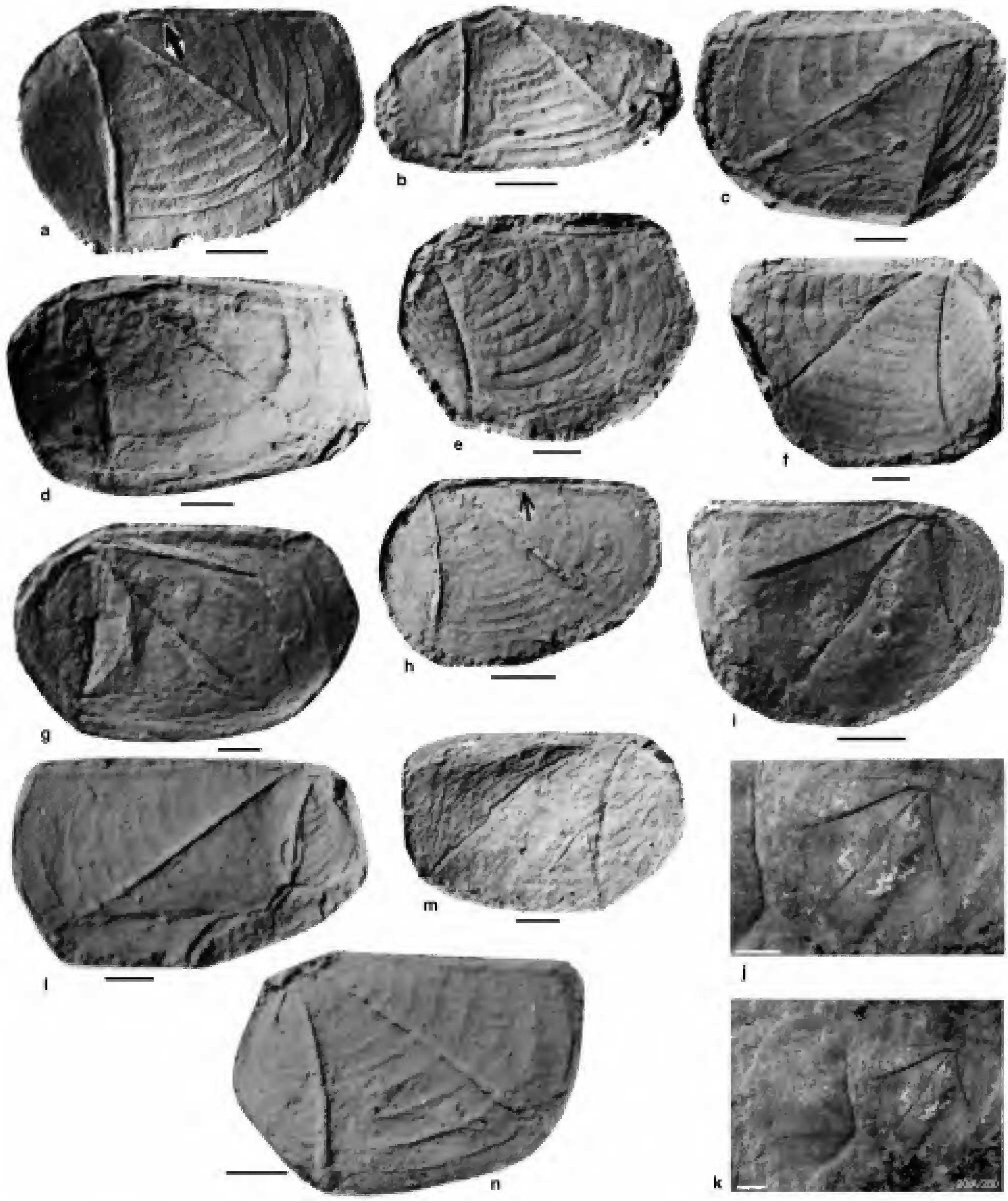

Figure 7. PERMIAN LEAIIDS, scale 1 mm. **a–n** *Hemicycloleaia mitchelli* (Etheridge): a—F 25459 (formerly *Leaia intermediata* Mitchell), internal mould of left valve; b—F 25463 (formerly *Leaia elliptica* Mitchell), internal mould of left valve; c—F 25421 (formerly *Leaia collinsi* Mitchell) internal mould of right valve; d—F 25461 (formerly *Trileaia sulcata* Kobayashi), external mould of right valve; e—F 25449 (formerly *Leaia pincombei* Mitchell) external mould of right valve; f—F 25426, external mould of left valve; g—F 25427 (formerly *Trileaia etheridgei* Kobayashi), external mould of right valve; h—holotype F 25487, internal mould of left valve, arrow points to embryonic rib sometimes present; i–k—F 25429 (formerly *Leaia belmontensis* Mitchell), external mould of a left valve overlies a fragment of an underlying valve, showing an associated complete right valve with only two major radial… [continued]

Growth bands broad and flattened, 10–17 in number. Umbo, small or moderate in size; two main radial carinae cross it, but do not converge on this area.

Remarks. Tasch (1987) proposed one new species, *Leaia (Leaia) oblongoidea* (pl. 24, fig. 1; pl. 40, fig. 8), based on an incomplete carapace. This species is obviously invalid for two reasons. First is a confusion over catalogue numbers in the plate explanation (Tasch, 1987, pl. 40) where F 25423 is given for *Leaia (Leaia) oblonga* (fig. 7) and F 25420 is given for *L. (Leaia) oblongoidea* (fig. 8). This is incorrect and the catalogue numbers should be reversed. Secondly, there is a discrepancy between pages 83 and 124 of Tasch's citations of Mitchell's plate and figure references. The synonymy given on page 83 for *oblongoidea* is incorrect, and should be reversed i.e., *L. (Leaia) oblongoidea* = *Leaia oblonga* Mitchell, 1925 (p. 441, pl. 41, fig. 5 *non* pl. 43, fig. 18). Finally, on page 124 there is an error (possibly typographic) in the citation of *L. oblonga* Mitchell, p. 441, pl. 41, fig. 3. Plate 41, fig. 3 refers to *L. intermediata* Mitchell; presumably Tasch meant plate 41, fig. 5, which illustrates the syntype (F 25420) of *L. oblonga.*

From our re-examination of Mitchell's type species in the Australian Museum, Sydney, all 16 of the abovementioned species can be divided into two groups according to their configuration of carapace valve: the subovate form including *Leaia mitchelli, L. collinsi, L. elliptica, L. etheridgei, L. oblonga, L. oblongoidea, L. ovata, L. paraleidyi, L. pincombei, L. (H.) immitchelli, L. (H.) kahibahensis* and *L. (H.) magnumelliptica*; the subcircular form including *L. discoidea, L. compta, L. latissima, L. quadrata* and *L. quadriradiata*. Previously Tasch (1987) referred *Trileaia belmontensis* (Kobayashi) and *Leaia intermediata* to *L. (H.) mitchelli*, because there is no third main radial carina on the valve, except the dorsal carina for *belmontensis*. This incorrect understanding (Kobayashi, 1954) was due to another overlapping valve, and the new photograph in the present paper (Fig. 7k) shows that an associated valve with the holotype (F 25429) has only two main radial carinae. In the same monograph Tasch also referred *L. quadriradiata* to *L. (H.) mitchelli*. For all Mitchell's type specimens of subovate form, the two main radial carinae start from the umbo area and reach to or near the ventral margin of the valve, but the anterior radial carina of *L. quadriradiata* fades out above the ventral margin (Fig. 8f,h). This character is very similar in *L. discoidea* (Fig. 8f,h), and therefore it should be transferred from *L. mitchelli* to the subcircular form. Mitchell (1925) noted that there are two short embryonic ribs near the dorsal margin in "*quadriradiata*", a character used by Novozhilov (1952) and Kobayashi (1954) to introduce their respective genera *Brachioleaia* and *Quadrileaia*. However, the presence of embryonic ribs, as in "*mitchelli*" is an unstable character, and does not merit taxonomic recognition (Tasch, 1987).

A revised list of plate explanations in Tasch's (1987) monograph concerning Mitchell's type material is provided as an appendix to this paper.

Type locality and horizon. Chert Quarry near Belmont, NSW (Mitchell, 1925); Upper Permian Boolaroo Formation.

Hemicycloleaia discoidea (Mitchell, 1925)

Fig. 8a–d,f,h

1925 *Leaia discoidea* Mitchell, p. 441, pl. 41, fig. 6, pl. 43, fig. 22.
1925 *Leaia compta* Mitchell, p. 444–445, pl. 42, fig. 14.
1925 *Leaia latissima* Mitchell, p. 444, pl. 42, fig. 11.
1925 *Leaia quadriradiata* Mitchell, p. 441–442, pl. 41, fig. 7.
1952 *Cycloleaia discoidea* (Mitchell); Novozhilov, p. 1361–1371, fig. 2a. (= drawing of Mitchell, 1925, pl. 41, fig. 6).
1952 *Brachioleaia quadriradiata* (Mitchell); Novozhilov, p. 1372, fig. 3v (= drawing of Mitchell, 1925, pl. 41, fig. 7).
1954 *Discoleaia discoidea* (Mitchell); Kobayashi, p. 108, 109, 141, 156.
1954 *Discoleaia discoidalis* [sic] (Mitchell); Kobayashi, p. 142, text-fig. 30f (= drawing of Mitchell, 1925, pl. 43, fig. 22).
1954 *Leaia compta* Mitchell; Kobayashi, p. 108, 155.
1954 *Leaia latissima* Mitchell; Kobayashi, p. 31, 108, 109,159.
1954 *Quadrileaia quadriradiata* (Mitchell); Kobayashi, p. 108, 109, 144, 164, text-fig. 30k. (= drawing of Mitchell, 1925, pl. 41, fig. 7).
1956 *Hemicycloleaia compta* (Mitchell); Novozhilov, p. 32, pl. 4, figs. 5–7 (= Mitchell, 1925, pl. 42, fig. 14).
1956 *Cycloleaia discoidea* (Mitchell); Novozhilov, p. 78, pl. 14, fig. 2 (= Mitchell, 1925, p. 441, pl. 41, fig. 6).
1956 *Cycloleaia cyclica* Novozhilov, p. 78, pl. 14, fig. 3 (= *Leaia discoidea* Mitchell, 1925, pl. 43, fig. 22).
1956 *Brachioleaia quadriradiata* (Mitchell); Novozhilov, p. 75, pl. 13, fig. 5 (= Mitchell, 1925: 441–442, pl. 41, fig. 7).
1958 *Cycloleaia discoidea* (Mitchell); Novozhilov, Tasch, p. 1100.
1987 *Cycloleaia discoidea* (Mitchell); Novozhilov, Tasch, p. 79, 123, pl. 22, fig. 1, pl. 40, fig. 6.
1987 *Leaia (Hemicycloleaia) compta* Mitchell; Tasch, p. 126, pl. 41, fig. 5.
1987 *Leaia (Hemicycloleaia)* cf. *compta* Mitchell; Tasch, p. 80, pl. 22, fig. 4.
1987 *Leaia (Hemicycloleaia) latissima* Mitchell; Tasch, p.125, pl. 41, fig. 2.
1987 *Leaia (Hemicycloleaia) mitchelli* (?) Etheridge; Tasch, p. 121, pl. 40, fig. 5.

Lectotype. External mould of left valve (F 25419) described by Mitchell (1925: 441, pl. 43, fig. 22); by subsequent designation in Kobayashi (1954: 143) [*non* Tasch, 1987: 123].

[Figure 7, continued]… carinae and a dorsal carina; l—F 25420 (formerly *Leaia oblonga* Mitchell), internal mould of an incomplete right valve; m—F 25456 (formerly *Leaia ovata* Mitchell), external mould of left valve; n—F 25454 (formerly *Leaia paraleidyi* Mitchell), internal mould of left valve. All specimens are from the Upper Permian Boolaroo Formation of the Newcastle Coal Measures, Sydney Basin, NSW. In this figure a–i, l–n reproduced from Fossil Conchostraca of the Southern Hemisphere and Continental Drift; Paleontology, Biostratigraphy and Dispersal by P. Tasch (1987), *Geological Society of America Memoir* 165; used by permission of the Geological Society of America.

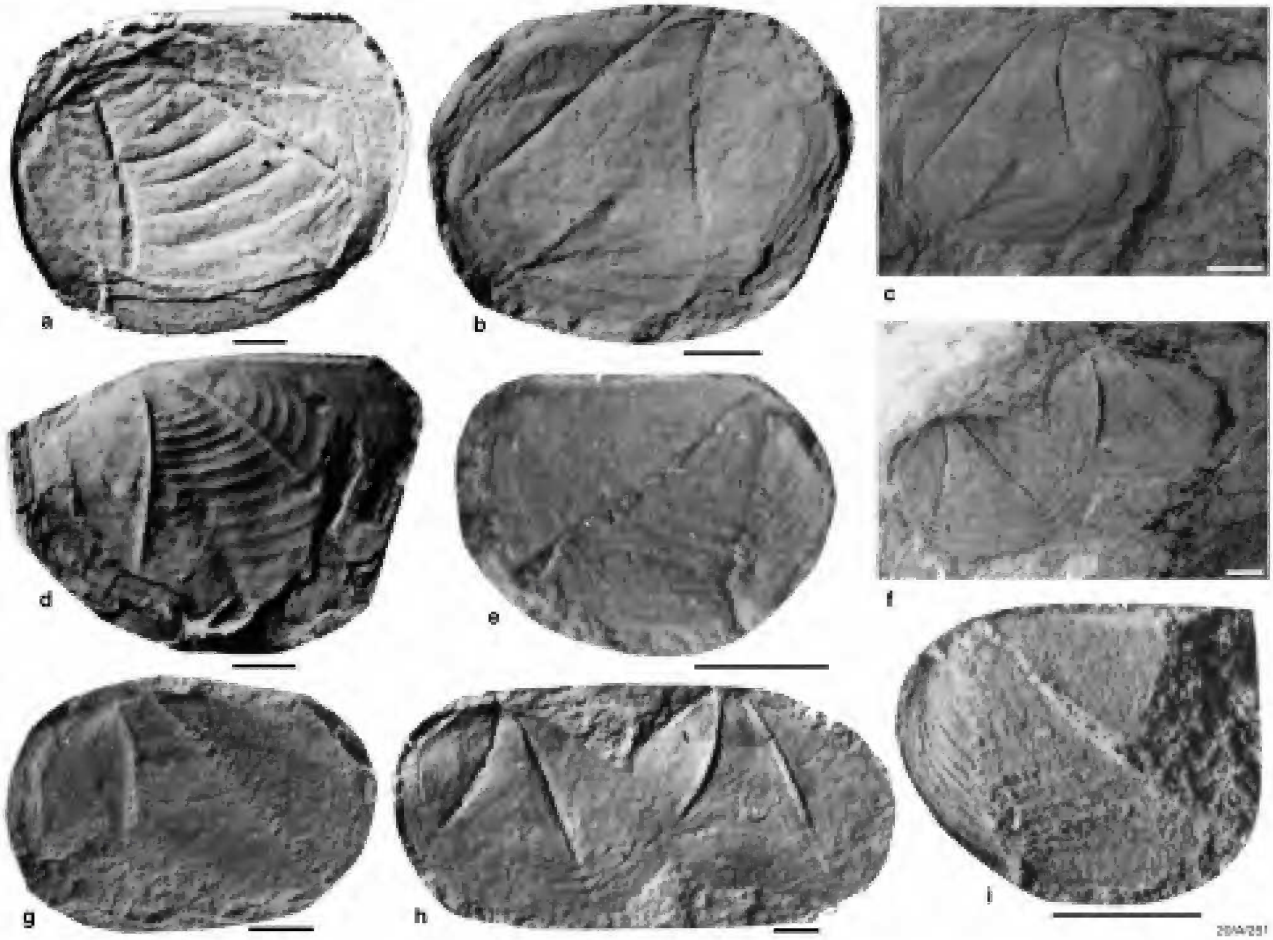

Figure 8. PERMIAN LEAIIDS, scale 1 mm. **a–d,f,h** *Hemicycloleaia discoidea* (Mitchell): a—F 25466 (formerly *Leaia latissima* Mitchell), external mould of right valve; b—lectotype F 25419, external mould of left valve; c—new photograph; d—F 25424 (formerly *Leaia compta* Mitchell), internal mould of left valve; f,h—F 25465 (formerly *Leaia quadriradiata* Mitchell), external mould of right valve on the left side and internal mould of left valve on the right side. Specimens from the Upper Permian Boolaroo Formation of the Newcastle Coal Measures, Sydney Basin, NSW. **e,g,i** *Hemicycloleaia deflectomarginis* (Tasch): e—holotype CPC 17173B, external mould of left valve; g—CPC 17174, (formerly *Leaia (H.)* sp. indet. 1 Tasch), internal mould of left valve; i—CPC 17173A, internal mould of holotype. Specimens from 4.2 km SSW of Winchester Homestead, Clermont, Bowen Basin, Blackwater Group. In this figure a,b,d and h are reproduced from Fossil Conchostraca of the Southern Hemisphere and Continental Drift; Paleontology, Biostratigraphy and Dispersal by P. Tasch (1987), *Geological Society of America Memoir* 165; used by permission of the Geological Society of America.

Diagnosis. Carapace moderate to large, subsemicircular or subcircular in outline, 4.2–8.0 mm long, 3.0–6.5 mm high. Growth bands broad and flattened, about 15 in number. Anterior radial carina gently curved and fades out above the ventral margin of valve. Posterior radial carina slightly straight and reaches near the ventral margin; both cross the umbo but do not meet. Sometimes the umbo is rather prominent (Fig. 8d). Dorsal margin frequently thickened to a thin carina. Rare occurrence of two short embryonic ribs near the dorsal margin and umbo area (Fig. 8f,h).

Remarks. Novozhilov (1952) proposed the genus *Cycloleaia* based on one of the two syntypes of *Leaia discoidea* Mitchell (1925: 441, pl. 41, fig. 6). Tasch (1987: 123) claimed that this specimen "has been lost and is no longer available for reference". The specimen (F 25422), however, has been studied by the present authors. Kobayashi (1954: 143) by subsequent designation, selected the second syntype (F 25419) figured by Mitchell (1925, pl. 43, fig. 22) as the holotype [sic] of *Leaia discoidea*, which he used as the type species for *Discoleaia*. As Novozhilov (1956) later introduced *Cycloleaia cyclica* based on this specimen (F 25419), the name of this species becomes an objective junior synonym of *Hemicycloleaia discoidea*.

The features of both syntypes (F 25419, F 25422) are very similar to *Hemicycloleaia mitchelli* except for the growth lines, which Novozhilov (1956) considered to be obscure or absent. According to Tasch (1987) and from our examination, the syntype (F 25422) designated the holotype, is a poorly preserved specimen of an external mould of the left valve, with about 15 growth bands. Thus, we regard *Cycloleaia* Novozhilov, 1952 as a junior synonym of *Hemicycloleaia* Raymond, 1946.

Mitchell (1925) also described three other species of *Leaia* having a subcircular or subsemicircular carapace with two major radial carinae, of which the anterior one fades out above the ventral margin. They are *L. compta, L. latissima* and *L. quadriradiata*, which on the basis of page priority in his paper, we regard as synonyms of *Hemicycloleaia discoidea*.

This species differs from *H. mitchelli* only in the configuration of the carapace valve. It is very similar to the two, previously discussed, species of *Hemicycloleaia* from the Early Carboniferous of the Canning Basin. *Hemicycloleaia mitchelli* and *H. discoidea* might be regarded as dimorphs within a single population, but their carapaces are larger, and their growth bands are broader, but reduced in number, when compared to the Early Carboniferous taxa.

Type locality and horizon. Chert Quarries near Belmont, NSW (Mitchell, 1925); Upper Permian Boolaroo Formation.

Other locality. Merewether Beach; from just above Dirty Seam (Mitchell, 1925); Upper Permian Lambton Formation.

Hemicycloleaia deflectomarginis (Tasch, 1979)

Fig. 8e,g,i

1979 *Leaia (Hemicycloleaia) deflectomarginis* Tasch, p. 40, pl. 6, figs. 1,2.
1979 *Leaia (Hemicycloleaia)* sp. indet. 1, Tasch, p. 40, pl. 6, fig. 3.
1987 *Leaia (Hemicycloleaia) deflectomarginis*; Tasch, p. 85.
1987 *Leaia (Hemicycloleaia)* sp.; Tasch, p. 85.

Diagnosis. Carapace small to moderate size, subovate in outline. 2.9–6.1 mm long, 2.0–3.2 mm high. Anterior radial carina slightly curved, posterior radial carina straight, both reaching the ventral margin; dorsal margin not thickened into a carina. 10–13 or more growth bands.

Remarks. Tasch (1979) described three leaiid specimens from the Late Permian of the Bowen Basin, Queensland as *Leaia (Hemicycloleaia) deflectomarginis* and *Leaia (Hemicycloleaia)* sp. indet. Of these specimens, one (CPC 17173B) is the external mould of another (CPC 17173A), and there are no perceptible taxonomic differences between these and the one referred to *Leaia (Hemicycloleaia)* sp. indet. (CPC 17174). This single species differs from *H. mitchelli* and *H. discoidea* in having a smaller carapace, narrower growth bands, and especially the lack of a dorsal carina.

Type locality and horizon. 4.2 km SSE of Winchester Homestead, Clermont area, Bowen Basin, Queensland. Upper Permian Blackwater Group (topmost Fort Cooper Coal Measures).

Family **Rostroleaiidae** Novozhilov, 1956

[*Nom. transl.* Shen, 1978; *ex* Rostrolealinae Novozhilov, 1956]

Diagnosis. Leaioidea with posterodorsally recurved growth bands along dorsal margin, and one to five radial carinae.

Genus ***Rostroleaia*** Novozhilov, 1952

1952 *Rostroleaia* Novozhilov
1954 *Falsirostria* Novozhilov
1954 *Granirostria* Novozhilov
1969 *Rostroleaia* Novozhilov; Tasch
1976 *Rostroleaia* Novozhilov; Zhang, Chen & Shen
1979 *Rostroleaia* Novozhilov; Tasch & Jones
1985 *Rostroleaia* Novozhilov; Chen & Shen
1987 *Rostroleaia* Novozhilov; Tasch

Type species. *Rostroleaia martynovae* Novozhilov, 1952: 369, fig. 1 (by original designation); Upper Permian (Kazanian), Nikolaevsk Gorge, Kargaline Mine, Ural Mountain Region, at the boundary with the Kungurian.

Diagnosis. Rostroleaiidae with elliptical carapace and two radial carinae. The dorsal margin thickened into a third carina. Growth bands gently recurved near the dorsal margin in the posterodorsal sector or this sector prolonged sharply.

Range. Middle Devonian to Upper Permian.

Distribution. China, Russia, England, USA and Australia.

Rostroleaia carboniferae (Tasch, 1979)

Fig. 6j–o

1979 *Limnadiopsileaia carboniferae* Tasch, p. 14, pl. 2, figs. 6–8.
1979 *Rostroleaia* sp. Tasch, p. 14, pl. 2, fig. 5.
1987 *Limnadiopsileaia carbonifera* [sic]; Tasch, p. 79.
1987 *Rostroleaia* sp.; Tasch, p. 79.

Diagnosis. Carapace small, elliptical to ovate in outline, with two radial carinae. Dorsal margin thickened into a third carina and posterior growth lines gently recurved in the posterodorsal sector (Fig. 6l,o). Growth bands broad and flattened, about 15 in number.

Topotype. Left valve and its external mould (CPC 33823) taken from the original collection, but not from the type series.

Remarks. This species was first assigned to *Limnadiopsileaia*, a genus based on a species the holotype of which is characterised by a single posterior radial carina. Its holotype (CPC 17141, Fig. 6k,l) is a broken left valve. Because the anterodorsal part of the external mould of its right valve exposes an anterior radial carina (Fig. 6k), we transfer this species to *Rostroleaia*. This reassignment is supported by evidence from a specimen (CPC 33823; Fig. 6m–o) selected from the original collection in AGSO.

Type locality and horizon. Grant Range No. 1 Well, core 52 (7907–7912 feet); Lower Carboniferous Anderson Formation.

Biostratigraphic implications of Australian Leaioidea faunas

Early Carboniferous Leaioidea

In the Canning Basin, *Hemicycloleaia andersonae* (Tasch, 1979), *H. grantrangicus* (Tasch, 1979) and *Rostroleaia carboniferae* (Tasch, 1979) are found only in Grant Range No. 1 Well (Fig. 3), where they are distributed over an interval of 192 m (7907–8537 feet) at the top of the Anderson Formation. Öpik (in McWhae *et al.*, 1958) regarded this *Hemicycloleaia* sequence as Late Carboniferous (Westphalian–early Stephanian) in age, but older occurrences of this genus are known. Copeland (1957) showed that *Hemicycloleaia* of the *tricarinata* species-group is present in the Namurian of eastern Canada. Also, *H. grantrangicus* is present in the Drummond Basin, Queensland, in the Raymond Formation, which is early Viséan, possibly late Tournaisian in age (this paper). In palynostratigraphic terms, the type interval is within the *Grandispora maculosa* Assemblage (Kemp *et al.*, 1977), as identified by C.B. Foster (pers. comm.) in core 64 (8544–8554 feet), and reported by Playford & Powis (1979) in core 50 (7502–7505 feet) and core 48 (7101–7103 feet). The *G. maculosa* Assemblage is apparently as old as middle Viséan in New South Wales, and as young as earliest Namurian in the Bonaparte Basin of northwestern Australia (Roberts *et al.*, 1995; Jones, 1996). Below core 62 (8530–8536 feet) is a thick interval (3324 feet; 1013 m) apparently barren of conchostracans. *Hemicycloleaia* was recorded (J.G. Tomlinson, unpublished BMR file report, 6 October 1955) from cuttings taken from 11860–12000 feet, and although some downhole contamination is possible, we consider that recirculation of cuttings over such a thick interval, more than 1000 m, is highly unlikely. Thus, two distinct leaioid intervals are in the well. Both are preceded by marine limestone incursions; at 12590 feet (with brachiopod or bivalve impressions and crinoid ossicles), and 9788–9808 feet (core 72; with conodonts, including *Cavusgnathus* sp.; ostracods, including *Cavellina* spp., *Lichvinella* sp., *Paraparchites* sp.; eridostracans *Cryptophyllus* sp. B Jones, and bivalves). The younger marine incursion is also recognised in other wells e.g., Yulleroo 1 (2840–2890 feet; with conodonts *Cavusgnathus unicornis, Spathognathodus scitulus*, ostracods, and eridostracans *Cryptophyllus* sp. B Jones), and Barlee 1 (core 2, 2308–2325 feet) with conodonts (*Ozarkodina*-element), ostracods, and eridostracans (*Cryptophyllus* sp. B Jones). No ostracods were found in association with the conchostracan samples. We conclude that (i) the possible age range of the upper leaioid fauna is middle Viséan to early Namurian, and (ii) the first (early Viséan) appearance of *Hemicycloleaia* in Grant Range 1 is compatible in age with the presence of *Hemicycloleaia grantrangicus* in the Raymond Formation (?late Tournaisian to early Viséan) of the Drummond Basin.

Late Permian Leaioidea

Foster & Jones (1994) concluded that the use of conchostracan species for precise correlation within the Late Permian, is inhibited by insufficient detailed knowledge of their stratigraphic ranges and geographic distribution. Despite the inclusion of many of Mitchell's (1925, 1927) leaiid and "estheriid" species in faunal lists for the Tatarian of the Russian Platform (e.g., Olferev, 1974; Kozur, 1977; Molostovskaya, 1997), to our knowledge none have been figured. From the Russian literature available to us, we know of no published descriptions of leaioid species from the type Tatarian (*Triedrolophus tverdochlebovi* Molin, 1968 from the lower Tatarian is now excluded from the Leaioidea; Chen & Shen, 1985).

However, those of Mitchell's (1925) leaiid species figured and described by Novozhilov from the Lower Tungus Basin, northern Siberia, warrant further discussion. In addition, some of Mitchell's (1927) "estheriid" species figured and described by Novozhilov from the Lower Tungus and Nordvik Basins also merit consideration. Thus, our work suggests that some broad correlations can still be made, and confirms, in part, Novozhilov's (1970) correlation of the upper NCM (Belmont Series [sic]) with the Upper Tatarian.

Lower Tungus Basin (Fig. 9): The Late Permian conchostracans from the Newcastle Coal Measures (NCM) compare well to those described (Novozhilov, 1965) from the pyroclastic Korvunchan Series in the Lower Tungus Basin (Fig. 8). *Hemicycloleaia mitchelli* (Etheridge, 1892) is present in the lower part of the Bugariktin Suite, near the top of the Korvunchan Series, and was figured and referred by Novozhilov (1965) to the synonyms *Mimoleaia mitchelli* (Etheridge, 1892) Novozhilov, 1954 and *Leaianella paraleidyi* (Mitchell, 1925). The figured specimens (see synonymy list p. 233) appear to be the only ones to our knowledge that illustrate *Hemicycloleaia mitchelli* from the Former Soviet Union. *Mimoleaia belozerovi* Novozhilov, 1965 (pl. 7, figs. 1–4) is possibly synonymous with *H. mitchelli*. The only other leaiid species in the NCM, *H. discoidea* (Mitchell, 1925), may be present in the Bugariktin figured by Novozhilov (1965, text-fig. 70, and pl. 7, fig. 7) under the name *Brachioleaia? quadriradiata* (Mitchell, 1925). The lower part of the Bugariktin Suite also contains, amongst others, two estheriid taxa described by Mitchell (1927) from the NCM viz., *Palaeolimnadia glabra* [recorded as *L. (Limnadia) glabra*], and *Cyzicus (Euestheria) novocastrensis* [recorded as *Pseudestheria novocastrensis*] (Novozhilov, 1958, 1965, 1970). Other estheriid taxa were collected from lower in the Korvunchan Series from strata thought to belong to the Tutonchan Suite. These were listed by Novozhilov (1965: 45) as Mitchell's (1927) species *Pseudestheria obliqua, P. novacastrensis, P. linguiformis*, and *P. trigonellaris*. The host strata, however,

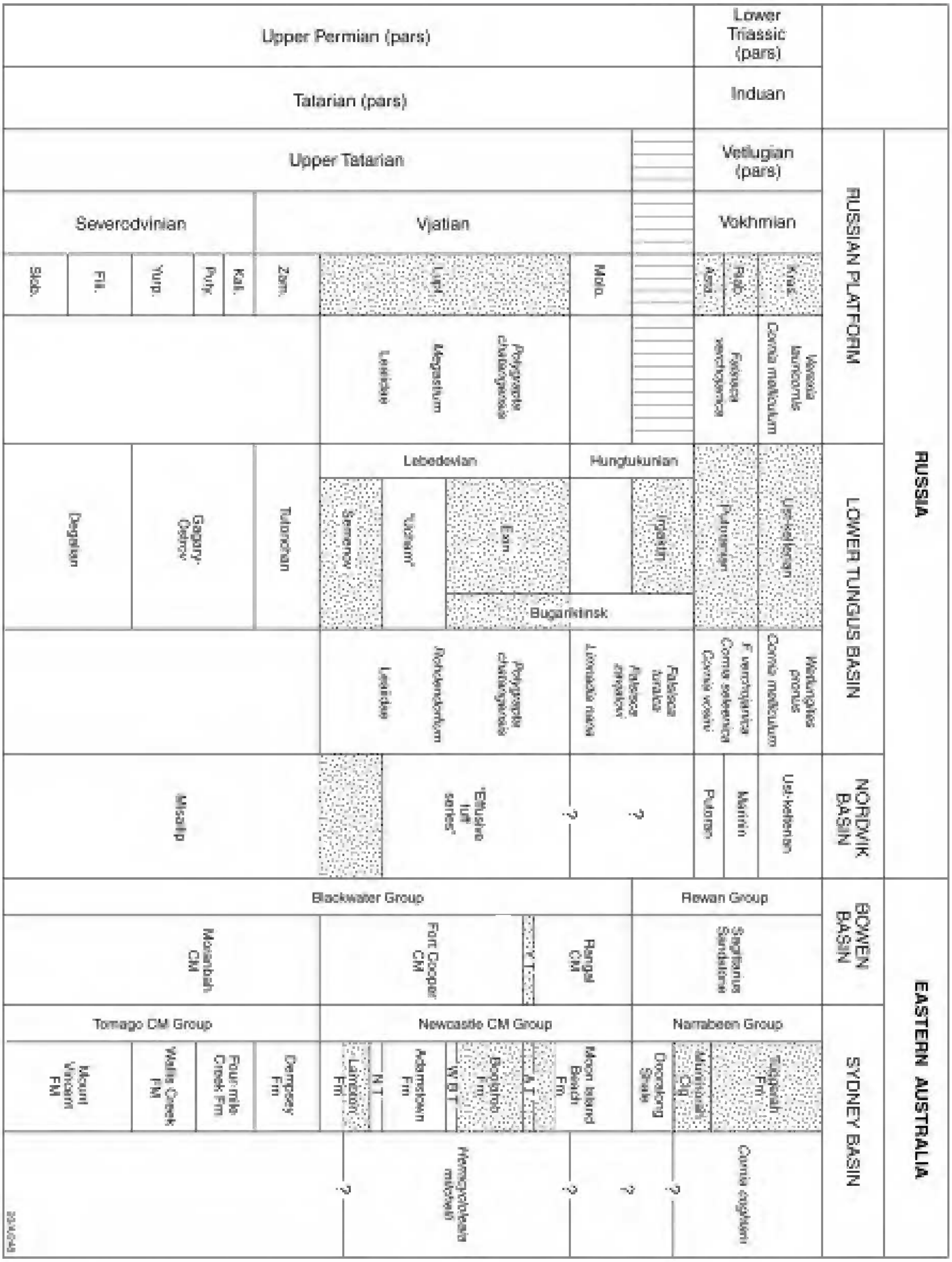

Figure 9. Correlation of the Upper Permian and lowest Triassic rocks of the Russian Platform, the Siberian Platform, and eastern Australia, based on Conchostraca. Russian data from Lozovsky, 1998. Stippled areas indicate sequences with conchostracan faunas. Abbreviations: members of Vokhmian horizon = Kras. (Krasnobakovian), Riab. (Riabinian), Asta. (Astashichian); members of Vjatian horizon = Molo. (Molomian), Lupt. (Luptugian), Zam. (Zamoshian); members of Severodvinian horizon = Kali. (Kalininian), Puty. (Putyatian), Yurp. (Yurpalovian), Fili. (Filian), Slob. (Slobobian). Abbreviation of names of tuff beds in eastern Australia: Bowen Basin, YT = Yarrabee Tuff; Sydney Basin, AT = Awaba Tuff (Formation), NT = Nobbys Tuff (Formation), WBT = Warner Bay Tuff (Formation).

are now known to be younger than authentic Tutonchan (Sadovnikov & Orlova, 1990, 1993; see below).

The stratigraphic nomenclature used by Novozhilov (1965, 1970), for the Korvunchan (Tuffogenic) Series, and followed above, has now been revised on the basis of megafloral, palynological and conchostracan studies (Gomankov & Meyen, 1986; Sadovnikov, 1997; Sadovnikov & Orlova, 1990, 1993, 1995; Orlova, 1990). Furthermore, new data on the field relationships of the Korvunchan (Tuffogenic) Series and the overlying Siberian Traps (Lozovsky, 1997, 1998), and geochronological studies of the Siberian Traps (Renne & Basu, 1991; Renne *et al.*, 1995; Kamo *et al.*, 1996), and the proposed Permian/Triassic boundary stratotype at Meishan, China, (Claoué-Long *et al.*, 1991, 1995; Renne *et al.*, 1995; Bowring *et al.*, 1998), have contributed to an improved understanding of the stratigraphic position of the Korvunchan conchostracans.

Correlation between the Lower Tungus Basin and the Russian Platform (Fig. 9): Sadovnikov & Orlova (1993) suggested on floral evidence, a correlation between the Gargaryostrov horizon, at the base of the Korvunchan Series, with the lower Upper Tatarian (Severodvinian). The overlying Tutonchan horizon is devoid of conchostracans, and is correlated by these authors to the uppermost Tatarian (Vyatian). The post-Tutonchan succession includes the Lebedevian horizon, the lower part of which contains the non-leaioid taxa listed above. These taxa previously thought by Novozhilov (1965: 45) to have come from the Tutonchan, were probably collected from the Semenov and Dyukin beds. The Exin beds of the uppermost Lebedevian horizon correspond to the lower part of the Bugariktin Suite which hosts the *Hemicycloleaia mitchelli* and non-leaioid fauna described by Novozhilov (1958, 1965, 1970). This conchostracan fauna extends upwards into the overlying Hungtukunian horizon of the Bugariktin Suite (Sadovnikov, 1997), and is replaced by a fauna dominated by *Falsisca turanica* (Novozhilov, 1965) in the upper part of the Bugariktin Suite (Irgaktin beds), at the base of the Putoranian Series (horizon). The overlying Nidym Suite in the lower Putoranian can be correlated with the Morongov suite of lavas at the base of the Upper Norilsk basalt (Lozovsky, 1997, 1998). As the minimum U-Pb age of the Morongov suite (251.2±0.3 Ma; Kamo *et al.*, 1996) is within analytical error of the proposed Permian/Triassic boundary stratotype at Meishan, China, for U-Pb ages of zircon (251.1±3.6 Ma, Claoué-Long *et al.*, 1991, 1995; 251.4±0.3 Ma, Bowring *et al.*, 1998) and for a 40Ar/39Ar age of sanidine (249.9±1.5 Ma, Renne *et al.*, 1995), it is reasonable to accept a Permian age for the Korvunchan conchostracans, because they are stratigraphically older than the inception of the Siberian Traps.

The floral evidence for the Sadovnikov & Orlova (1993) correlation mentioned above i.e., the Gargaryostrov horizon with the Severodvinian, and the Tutonchan horizon with the Vyatian, implies that the overlying Korvunchan leaioid fauna is either early Vyatian (Novozhilov, 1970) or possibly post-Tatarian, pre-Vetlugian (Sadovnikov & Orlova, 1993) in age. Sadovnikov (1997) and Sadovnikov & Orlova (1994, 1995) regarded the Lebedevian, Hungtukunian and Putoranian horizons to correspond to the hiatus between the Tatarian Stage and the Lower Triassic Velugian Stage of the Russian Platform, for which they proposed the Taimyrian Stage. However, on palynological evidence, this hiatus is probably much shorter than that envisaged by Sadovnikov & Orlova, and may be equivalent to the Hungtukunian only, as this horizon contains the *Triquitrites proratus* spore assemblage, which is absent from the Vyatian of the Russian Platform, but present in the upper Zechstein (Z6, Z7) of the German Basin (Yaroshenko, 1990), and is represented by the *Leiosphaeridea changxingensis-Micrhystridium stellatum* Assemblage Zone in the uppermost Changhsingian at Meishan, South China (Ouyang & Utting, 1990). This stratigraphic link is an important part of the correlation proposed by Lozovsky (1997, 1998), which is adopted in this paper (Fig. 6).

Nordvik Basin (Fig. 9): The conchostracan fauna at the top of the subsurface Misailap Series (Novozhilov, 1958) includes Mitchell's species *Palaeolimnadia glabra, Cyzicus (Euestheria) novocastrensis, C. (E.) obliqua*, and *Glyptoasmussia belmontensis*. This fauna is probably equivalent to the post-Tutonchan fauna [*Cyzicus (Euestheria) linguiformis, C. (E.) novacastrensis, C. (E.) obliqua* and *C. (E.) trigonellaris*] that was probably collected from younger (Semenov and Dyukin) beds in the lower part of the Lebedevian horizon in the Lower Tungus Basin (Sadovnikov & Orlova, 1990, 1993). Of these Mitchell (1927) species, *Cyzicus (Euestheria) novacastrensis* has been reported from the Severodvinian horizon of the Upper Tatarian stratotype sections of the Russian Platform (Olferev, 1974).

Correlation between the Nordvik Basin and the Russian Platform (Fig. 9): Lev (1957) correlated the non-marine ostracods (mostly new species of *Paleodarwinula*) from the *Darwinula arctica* beds of the Misailap and the overlying Effusive-Tuff Suite, with the Urzhum horizon (Early Tatarian) and the lowermost part of the Severodvinian horizon (earliest Late Tatarian) of the Russian Platform. This correlation is slightly older than the one advocated here, and suggests that the fauna needs to be redescribed. Pollen studied from the same deposits by Dibner (1958) were correlated with other Angaran assemblages regarded as Tatarian. However, it is uncertain whether these Angaran assemblages can be correlated with those of the type Tatarian of the Russian Platform (Gomankov & Meyen, 1986). Moreover, even in the northern Russian Plate there is still doubt about the palynological placement of the Kazanian-Tatarian boundary (Astafurov & Medvedeva, 1993).

Late Permian correlation between the Sydney Basin and the Lower Tungus and Nordvik Basins, northern Siberia (Fig. 9)

The presence of *Hemicycloleaia mitchelli, H. discoidea* and the estheriid species *Palaeolimnadia glabra* and *Pseudestheria novocastrensis* in the Belmont localities in the upper part of the NCM (Boolaroo Formation) indicates a correlation with these taxa described by Novozhilov from the lower part of the Bugariktin Suite (= Exin beds, at the top the Lebedevian) of the Lower Tungus Basin. This comparison parallels the similarity between the Belmont insect fauna of the upper NCM and that of the Angara province (Riek, 1970).

The estheriid species *Cyzicus (Euestheria) linguiformis, C. (E.) novacastrensis, C. (E.) obliqua*, and *C. (E.) trigonellaris* in the Merewether Beach locality in the lower part of the NCM (Lambton Formation) can be correlated with those collected from the lower Lebedevian Semenov and Dyukin beds of the Lower Tungus Basin. Similarly, these species indicate a correlation with those from the subsurface Misailap Series in the Nordvik Basin (Novozhilov, 1958, 1965) described and figured as *Palaeolimnadia glabra, Cyzicus (Euestheria) novocastrensis, C. (E.) obliqua*, and *Glyptoasmussia belmontensis*.

In summary, the Late Permian leaioid and estheriid faunas of the Newcastle Coal Measures of the Sydney Basin are correlated with those of the Lebedevian of the Lower Tungus and Nordvik Basins, northern Siberia, which in turn, indicate a correlation with the Late Tatarian Vjatian (Luptug member) horizon of the Russian Platform (Lozovsky, 1998).

Molostovskaya (1997) listed *Hemicycloleaia intermediata*, and *Siberioleaia oblonga*, both junior synonyms of *Hemicycloleaia mitchelli*, in the Late Tatarian (Severodvinian) conchostracan fauna of the Russian Platform. If this is confirmed, and if the correlation presented here (Fig. 9) is correct, with further work, we would expect to find *H. mitchelli* within the Tomago Coal Measures.

The palaeobiogeographic distribution of Mitchell's (1925, 1927) Late Permian (Tatarian) conchostracan species in the Siberian Platform, Russian Platform, and eastern Australia requires an explanation. The Russian species could be different to those of Mitchell, but show an ecophenotypically similar carapace morphology, and reflect the bipolar distribution of cool waters at that time. Alternatively, if they are conspecific, the distribution of land and sea, according to current Late Permian palaeogeographic reconstructions (e.g., Erwin, 1994; Golonka *et al*., 1994; Scotese & McKerrow, 1990), would have allowed migration to take place. Tasch (1987) envisaged a non-marine, interlacustrine dispersal, originally as wind-transported eggs, between the Siberian Platform, Russian Platform, and eastern Australia via China. We speculate, without necessarily extrapolating the lacustrine milieu of extant conchostracan species to Palaeozoic species, that they may have lived in estuaries and ephemeral relict water bodies along a coastal plain, where their eggs could be dispersed by wind, and by minor marine incursions. We find it difficult to exclude the possibility that marginal marine influences played some role, however minor, in the distribution of those of Mitchell's (1925, 1927) conchostracan "species" identified in the Late Permian of Russia (Novozhilov, 1956, 1965).

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Appendix

A revised list of plate explanations in Tasch's (1987) monograph concerning Mitchell's type material.

Page 228, pl. 40, fig. 2, the holotype of *Leaia mitchelli* Etheridge, is an internal mould of a left valve [not right valve]; fig. 3, the holotype of *Leaia collinsi* Mitchell is an internal mould of a right valve [not right valve]; fig. 5, length of valve of *Leaia quadriradiata* Mitchell is 4.2 mm [not 6.5 mm]; fig. 7 and 8, the catalogue number (F 25420 and F 25423) should be reversed.

Page 230, pl. 41, fig. 1, t, the holotype of *Leaia intermediata* Mitchell is an internal mould of left valve [not left valve]; fig. 4, the holotype of *Leaia belmontensis* Mitchell is an external mould of left valve [not external mould of right valve]; fig. 6, the holotype of *Trileaia etheridgei* Kobayashi is an external mould of right valve [not left valve]; fig. 7, the holotype of *Leaia elliptica* Mitchell is an internal mould of left valve [not external mould of left valve].

Page 232, pl. 42, fig. 8, the holotype of *Leaia paraleidyi* Mitchell is an internal mould of left valve.